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Determining Scaphirhynchus Sturgeon Population Demographics and Dynamics: Implications for Range-Wide Management, Recovery, and Conservation

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DETERMINING *SCAPHIRHYNCHUS* STURGEON POPULATION DEMOGRAPHICS AND DYNAMICS: IMPLICATIONS FOR RANGE-WIDE MANAGEMENT, RECOVERY, AND CONSERVATION

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DETERMINING *SCAPHIRHYNCHUS* STURGEON POPULATION DEMOGRAPHICS AND DYNAMICS: IMPLICATIONS FOR RANGE-WIDE MANAGEMENT, RECOVERY, AND CONSERVATION

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Sturgeons (Acipenseridae) have experienced world-wide declines as a result of anthropogenic effects such as over-harvest, habitat degradation, altered flow regimes, and pollution. Nearly all European and Asian sturgeon species have experienced population declines and have subsequently been classified as either threatened or endangered. North American sturgeons have experienced a similar plight in that all eight native sturgeon species are listed as endangered, threatened, or of special concern. Direct linkages between North American sturgeon declines and anthropogenic effects are difficult to assess due to scale considerations, fluctuating environmental conditions, difficulty in capture, and the interaction of all these effects. To recover, restore, or maintain abundance of these species across their range, thorough knowledge of life history characteristics or strategies, population dynamics, and population connectivity for each species is imperative. In this dissertation, I use data from local (Platte and Missouri Rivers, Nebraska) to nearly range-wide scales to describe components of *Scaphirhynchus* sturgeon population dynamics and demographics and assess various analyses typically used for calculation of dynamic rate functions.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: INTRODUCTION

Sturgeons (Acipenseridae) have experienced world-wide declines as a result of a combination of anthropogenic effects such as over-harvest, habitat degradation, altered flow regimes, and pollution (Birnstein 1993). Sturgeons are highly migratory, long-lived, late-maturing fishes that do not spawn annually; a unique combination of traits that make them highly susceptible to human activities (Birnstein 1993; Birnstein et al. 1997; Pikitch et al. 2005). Nearly all European and Asian sturgeon species have experienced population declines and have subsequently been classified as either threatened or endangered, and several species will likely become extinct in the near future (e.g., *Acipenser dabryanus*, *Psephurus gladius*; Birnstein 1993). North American sturgeons have experienced a similar plight in that seven of eight native sturgeon species are listed as endangered, threatened, or of special concern (Williams et al. 1989; Jelks et al. 2008).

There are three North American species that are classified as river sturgeons (genus *Scaphirhynchus*); these are the shovelnose sturgeon *S. platorynchus*, pallid sturgeon *S. albus*, and Alabama sturgeon *S. suttkusi*. Both pallid sturgeon (listed in 1990) and Alabama sturgeon (listed in 2000) are federally listed as endangered due to range-wide declines linked to construction of dams, commercial harvest, and modification of rivers for navigation (Bailey and Cross 1954; Birnstein 1993; Keenlyne 1997; Mayden and Kuhajda 1997). Pallid sturgeon and shovelnose sturgeon are sympatric throughout major portions of their geographic range and will be the species of focus for this dissertation. A recovery plan was formulated to ensure the remaining wild pallid sturgeon were protected from harm, harassment, or death (Dryer and Sandvol 1993). A

captive broodstock and stocking program was created to augment the declining population and habitat restoration efforts have been initiated (e.g., creation of shallow water habitat, flow modifications, etc.).

Shovelnose sturgeon are the most abundant and widespread of North American sturgeons and inhabit the large river systems throughout the Mississippi River and Missouri River drainages (Bailey and Cross 1954; Keenlyne 1997), yet, commercial harvest and habitat degradation have reduced their distribution and abundance (Keenlyne 1997; Koch and Quist 2010). Shovelnose sturgeon are classified as extirpated or at risk of extirpation in 50% of the states within their native distribution and many states have indicated either a decline in abundance or an unknown status (Keenlyne 1997; Koch et al. 2009). Due to their similarity in appearance to pallid sturgeon, the U.S. Fish and Wildlife Service eliminated harvest of shovelnose sturgeon by commercial fishers in 2010 from areas where the two sturgeon species are sympatric.

Data Gaps for Sturgeon Recovery or Sustainability

Anthropogenic disturbances have been hypothesized to be primary drivers in the declines of *Scaphirhynchus* sturgeons (Birnstein 1993 and others). However, direct linkages between population declines and anthropogenic effects are difficult to assess due to scale considerations, fluctuating environmental conditions, difficulty in collecting fish, and the interaction of all these effects (Bunn and Arthington 2002; Secor et al. 2002; Hamel et al. 2009; Poff and Zimmerman 2010). Recent work has characterized how anthropogenic disturbances affect reproductive behavior of *Scaphirhynchus* sturgeons (DeLonay et al. 2007; DeLonay et al. 2009; Goodman et al. 2012); however, information

such as early life history traits such as habitat requirements, movement within and among river systems, home-range requirements, population size, and general population dynamics is needed to identify population-level responses to management actions.

Data Gaps -Hydrology

The flow in a river can be considered the single most important variable that dictates the distribution and abundance of riverine fishes and regulates the ecological integrity of flowing water systems (Southwood 1988; Poff and Allan 1995; Poff et al. 1997; Pusey et al. 2000; Kennard et al. 2007; among others). Moreover, long-term variability in river discharge (i.e., frequency, timing, magnitude, duration, and rate of change) is fairly predictable and is what defines the physical habitat found over large spatial scales (Pegg and Pierce 2002a; Kennard et al. 2007). A single river can consistently provide episodic, seasonal, and persistent types of habitat based on variation in the natural flow regime. These variable flow conditions determine the spatial variability and connectivity of habitats that, in turn, influence local colonization and extinction events. This diversity of habitat types has promoted the evolution of species that exploit the habitat created and maintained by hydrologic variability (Poff and Allan 1995).

Just as the natural flow regime is directly involved in determining fish assemblages in rivers and streams, the temporal patterns in annual flow variability is directly related to the growth, reproduction, and recruitment of native fishes (Bunn and Arthington 2002). Many characteristics of the life cycle of a particular species of fish are linked to the flow regime. For example, spawning behavior (i.e., reproduction) in some

lotic species is triggered by peak discharge events during the spring (DeLonay et al. 2007; Goodman et al. 2012). During peak flows, lotic species make upstream migrations allowing sufficient distance for larvae to drift back downstream and recruit to the population. Peak flows also allow lateral expansion into the floodplain, providing nursery habitats for young and providing allochthonous energy inputs for growth and survival (Poff et al. 1997; Bunn and Arthington 2002; Kennard et al. 2007). Ultimately, these flow events, coupled with ideal environmental conditions (i.e., temperature), create optimal situations for a variety of life stages or strategies that have adapted to these dynamic environments.

Alterations to the hydrology of rivers and streams such as damming, channelization, or water withdrawals directly impact ecological processes (Malmqvist and Rundle 2002 and others). An altered flow regime changes the established patterns of natural hydrologic variation and disturbance and creates new conditions in which the native biota may be poorly adapted (Poff et al. 1997). Extreme daily variations, such as those produced by power generation, have no natural equivalent and many aquatic populations suffer high mortality rates due to stress from wash-out or from being stranded during low flow periods. Similarly, streams with low streamflow variability have very different fish assemblages than streams with high variability (Meador and Carlisle 2012). In artificially fluctuating environments, riverine species with specialized adaptations are typically replaced by generalist species that can tolerate frequent and large fluctuations in flow (Poff and Allan 1995; Poff et al. 1997; Pusey et al. 2000; Pegg and Pierce 2002b). Many studies have noted shifts in native fish assemblages following modifications to the natural flow regime. Meador and Carlisle (2012) found a greater

loss of native species from sample sites that had reduced natural streamflow variability, and there was a strong relation with the severity of streamflow alterations to the probability of native species impairment. Mims and Olden (2013) examined fish assemblage alterations in response to modified flow regimes by large dams and reported flow modification that created a high degree of flow constancy (i.e., reduced natural variability) resulted in a shift in life-history strategies. For example, fish assemblages downstream of dams had a greater proportion of equilibrium species (common in more stable and predictable environments) and a lesser proportion of opportunistic species (common in an environment with unpredictable change). Sturgeon species are likely susceptible to changes in natural hydrologic variation as well because they possess traits that are well-suited for stochastic riverine environments (e.g., morphology, life expectancy, and intermittent spawning.). These traits have evolved over millions of years as sturgeon species represent a lineage (order: Acipenseriformes) dating back to the Lower Jurassic period (200 million years) (Pikitch et al. 2005). Therefore, there is a need to identify the particular components of the modified flow regime (e.g., reduced spring rise, altered temperature regime, and flow constancy) that may be responsible for where sturgeon are distributed and for population declines.

Data Gaps - Tributaries

Tributary streams are important components to main-stem rivers by providing use for fish spawning and reproduction, nursery or refuge habitat, complexity of habitat types, and areas for foraging (Dames et al. 1989; Osborne and Wiley 1992; Ponton and Copp 1997; Rice et al. 2001; Pracheil et al. 2009; Neely et al. 2010). Tributary streams play a functional role in the ecology of large rivers; however, the importance of tributary

streams is not completely understood. For example, some of the more highly regarded concepts in river ecology have largely overlooked the potential influences tributaries might have on energy inputs, fish species richness, and their spatial location within the river network (Vannote et al. 1980; Junk et al. 1989; Thorpe and Delong 1994). Tributary streams disrupt the linear pathway of unidirectional increases in species diversity and nutrient availability by creating discontinuities at tributary confluences (Rice et al. 2001; Kiffney et al. 2006). Confluences provide greater habitat complexity by providing higher substrate heterogeneity, greater stream depth, and increases in wood volume or abundance (Kiffney et al. 2006). Furthermore, tributary streams are often relatively unaltered compared to main-stem rivers and may provide a viable opportunity for conservation of large-river biota (Pracheil et al. 2013).

Little information currently exists on the importance of tributaries for completion of essential life stages for *Scaphirhynchus* sturgeon. Tributaries may be important for processes such as reproduction and rearing or for habitat types related to refuge and food consumption. Sturgeon species are known to exist in the lower Yellowstone River, Montana. Bramblett and White (2001) used telemetry to track movements of shovelnose sturgeon and pallid sturgeon throughout the year. Pallid sturgeon were found to move into the Yellowstone River during the spring and summer and return to the Missouri River during the fall and winter. Shovelnose sturgeon were ubiquitous users of the Yellowstone and Missouri rivers; however, movement patterns increased within the Yellowstone River during the spring. Similarly, telemetry research in the Platte River, Nebraska has indicated increased use during the spring and summer periods with migrations to the Missouri River during the fall (Snook et al. 2002; Peters and Parham

2008). Pallid sturgeon have also likely spawned in the Platte River according to coinciding depth and temperature data recorded on a data storage tag that was implanted into the fish (DeLonay, USGS, *unpublished data*). While these studies have provided information on *Scaphirhynchus* sturgeon movement patterns in tributaries, particularly during the spawning season, it is largely unknown if tributary use is critical for completion of a particular life stage and the role that tributaries may play in metapopulation dynamics.

Data Gaps – Population Demographics and Dynamics

Understanding population demographics and dynamics is critical for recovery of rare or declining species. However, accurate information on sturgeon life history characteristics, behaviors, and population distribution and abundance are difficult to obtain due to the sturgeon's propensity to live long, spawn infrequently, and inhabit large, turbid river systems. Recent efforts have divulged much information towards the understanding of the ecology of *Scaphirhynchus* species; however, more information must be attained before populations can be sustained or recovered.

The specific factors that influence fish abundance and biomass are typically described by the dynamic rate functions - mortality, growth, and recruitment. An understanding of these population parameters is essential for demographic models used to predict population viability and responses to management actions (Bajer and Wildhaber 2007; Koch et al. 2009; Jager et al. 2010). Knowledge of the population age structure is a critical component needed for proper management of the fishery (Beamish and McFarlane 1983). Further, age-structured models are commonly used for determining

mortality rates (i.e., catch-curve), spawning potential ratio, and recruitment dynamics (Ricker 1975; Goodyear 1993; Slipke et al. 2002). Therefore, there is a need to assess accuracy and precision of age data for *Scaphirhynchus* species.

The leading edge of the pectoral fin ray is the most commonly used aging structure for *Scaphirhynchus* species. This structure can be removed non-lethally and has the highest reported precision compared to other structures (Jackson et al. 2007). However, the accuracy of pectoral fin rays (i.e., absolute age; Campana 2001) has not been successfully validated and several authors have reported use with caution (Whiteman et al. 2004; Jackson et al. 2007; Kennedy et al. 2007; Killgore et al. 2007). Several year classes of known-age pallid sturgeon exist due to the propagation of pallid sturgeon in hatcheries. Hurley et al. (2004) conducted an absolute age validation study by examining fin rays from 16, age-6 pallid sturgeon that were reared and held in captivity until fin ray removal. Results indicated low precision and accuracy; most age estimates were off by two years from the true age. To combat the affect captivity may have had on annulus formation, Koch et al. (2011) conducted a similar study with hatchery-reared individuals that were released into the wild during the first year of growth. The authors used 46 individuals from 6 different age groups (age-1 to age-7) of the 2001-2007 year classes. Precision between readers was low (30 to 36% exact agreements) and accuracy of age estimates among readers varied from 28 to 42%. Previous studies have attempted to validate fin rays as an aging structure for shovelnose sturgeon. Whiteman et al. (2004) and Rugg (2013) used marginal increment analysis to validate periodicity of annulus formation. Opaque bands are typically deposited on fin

rays of *Scaphirhynchus* species, but variability exists in both readability and consistent annual deposition.

Growth is commonly assessed throughout a fish's life by back-calculating fish body length from marks on aging structures. Back-calculation is a technique that uses measurements (i.e., distance) between annuli marks to infer individual length at an earlier time (Francis 1990). This technique is widely used in age and growth studies and is a simple method to increase the number of length-at-age data needed to calculate various growth curves (Francis 1990). However, the interpretation of age and growth from bony structures is based on the assumption that annuli are formed at a constant frequency and that the distance between annuli is proportional to fish somatic growth (Campana and Neilson 1985). Current recaptures from shovelnose sturgeon that were originally tagged in the late 1990's to early 2000's have displayed minimal somatic growth (i.e., approximately 4 mm annually; Hamel, M.J., *this study*). These observations infer that the assumption of proportional growth may be in violation and that poor precision reported in the literature may be an indication of inaccuracies.

Growth is an important attribute for fishes because it can directly relate to fish condition and habitat quality. Therefore, comparisons of growth between or among populations may provide insight into responses from management actions, habitat alterations, or restoration efforts. However, growth rates and maximum size (i.e., length) have been known to vary according to latitude (Conover and Present 1990). There are two competing hypothesis that describe how latitudinal compensation in growth might evolve. The first hypothesis states that genetic variation in growth rate is a response to an adaptation to temperature. Growth rates for populations living in alternate latitudes will

be maximized at the temperature most commonly experienced (Yamahira and Conover 2002). That is, fishes from high-latitude environments will have maximal growth rates at lower temperatures than fishes from low-latitudes and vice versa. The second hypothesis (i.e., counter gradient variation) focuses on length of the growing season rather than local mean temperature. Fishes living in high-latitude are subject to colder temperatures and, therefore, a shorter growing season. These individuals compensate for the shorter duration by evolving a higher overall capacity for growth. Maximal growth still occurs at the same temperatures as low-latitude individuals, but high-latitude fishes grow proportionately faster across all temperatures that permit growth (Conover 1990; Conover and Present 1990; Marcil et al. 2006). *Scaphirhynchus* sturgeon are found throughout the entire Missouri and lower Mississippi river basins; therefore, they have the capacity to express variation in growth rates across a broad latitudinal range. Growth may be an important variable for relating responses to various anthropogenic affects; therefore, it is important to characterize current range-wide growth patterns such as maximum length, growth per various length ranges, and at what size growth becomes minimal for *Scaphirhynchus* sturgeons.

Understanding mortality in fish populations is important for fisheries stock assessment and management. In many fisheries stocks, dividing mortality into deaths that are of natural causes (*M*) and deaths that are a result of fishing harvest (*F*) can be quite challenging. However, this information is vital when modeling stock size and the productivity or resiliency that can be obtained (Clark 1999). *Scaphirhynchus* sturgeon are highly susceptible to overharvest due to their propensity to live long and spawn infrequently (Boreman 1997; Quist et al. 2002; Colombo et al. 2007; Koch et al. 2009;

Tripp et al. 2009). Shovelnose sturgeon were commercially exploited throughout portions of their range until September of 2010, when they were protected under the U.S. endangered species act due to the similarity in appearance to the endangered pallid sturgeon. Prior to protection, harvest of shovelnose sturgeon for roe was common throughout parts of the lower Missouri River, the Mississippi River, and their tributaries. Harvest peaked at an all-time high of 60,000 kg in 2001 throughout the upper Mississippi River system (Colombo et al. 2007).

Several estimates of total, annual mortality (*A*) have been calculated for *Scaphirhynchus* sturgeon. Colombo et al. (2007) and Tripp et al. (2009) indicated that *A* for shovelnose sturgeon and pallid sturgeon were as high as 37-40% in the middle Mississippi River. Conversely, Quist et al. (2002) reported annual mortality rates as low as 10% for shovelnose sturgeon in the upper Missouri River. These estimates were calculated with an age-structured model (i.e., catch curve) that requires an accurate measure of age estimates derived from an aging structure (e.g., fin rays). It is unknown how erroneous age estimates might affect mortality estimates; however, several authors have shown that age-structured stock assessments are particularly sensitive to the chosen value of natural mortality (Mertz and Myers 1997; Clark 1999; Paragamian and Beamesderfer 2003). Few studies have examined alternative methods for calculating mortality. Using a standard mark-recapture Cormack-Jolly-Seber model, Steffensen et al. (2010) examined capture histories of each hatchery-reared pallid sturgeon cohort captured in the lower Missouri River to estimate annual survival rates (*S*). Survival (1-*A*) was low for age-0 pallid sturgeon ($S = 0.05$), but increased to 0.69 for age-1 fish and 0.92 for fish greater than age-1. Hadley and Rotella (2009) used mark-recapture data and

found similar results for pallid sturgeon in the upper Missouri River where age-1 pallid sturgeon had a survival rate of 0.75 and increased to 0.97 during their second year of life.

Mortality estimates may vary by location due to factors such as harvest, habitat degradation, or emigration. However, potential sources of error exist from mortality estimated from age-structured analysis. Sensitivity analysis from population viability models have shown that population growth rates were most sensitive to survival rates (Bajer and Wildhaber 2007). For example, a 5% increase in survival increased the population growth rate by 5% for shovelnose sturgeon (initial total mortality input was 25%) and 6% for pallid sturgeon (initial total mortality input was 7%) (Bajer and Wildhaber 2007). However, previous estimates of mortality from catch-curve and mark-recapture analyses within the same study area have contradicted each other, suggesting erroneous mortality calculations might have large impacts on the understanding of long-term viability of sturgeon species.

Study Objectives

This dissertation focuses on *Scaphirhynchus* sturgeon population ecology at various spatial scales to better understand the dynamics and ecological processes that govern species persistence. I begin by examining pallid sturgeon population characteristics in the Platte River, Nebraska; a large tributary to the Missouri River that receives little attention for species recovery efforts (Chapter 2). Various site-specific habitat components and river-wide environmental conditions were further explored to determine factors that dictate the presence of pallid sturgeon in the Platte River (Chapter 3). I next evaluated the efficacy of mark-recapture data from known-age, hatchery-reared

pallid sturgeon to validate age estimates and corroborate growth estimates generated from back-calculations obtained from sectioned pectoral fin rays (Chapter 4). The effects of inaccurate age determinations from fin rays were explored to assess how variability in age assignments would affect calculations of growth and total annual mortality, and ultimately, affect population demographic models used for recovery or sustainability of sturgeon (Chapter 5). The final research chapter of this dissertation focuses on an assessment of growth, maximum size, and an estimate of age from several populations of shovelnose sturgeon throughout their range-wide distribution to better understand growth characteristics and to identify populations of sturgeon that may be in further need of protection or rehabilitation (Chapter 6). Finally, I conclude with recommendations for *Scaphirhynchus* sturgeon conservation and management at both local and regional scales (Chapter 7).

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CHAPTER 2: POPULATION CHARACTERISTICS OF PALLID STURGEON IN THE LOWER PLATTE RIVER, NEBRASKA

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Summary

Pallid sturgeon *Scaphirhynchus albus* were federally listed as endangered in the United States of America in 1990 due to range-wide declines linked to dam construction, commercial harvest, and river modification for navigation. Pallid sturgeon have been intensively studied in recent years to combat a dwindling adult population that does not support natural recruitment; however, most of this effort has occurred in the main-stem Missouri and lower Mississippi rivers. Pallid sturgeon are known to occupy tributary streams intermittently, but the importance of tributaries for completion of essential life stages for pallid sturgeon is unknown. Tributary streams may provide use for fish spawning and reproduction, nursery or refuge habitat, and areas for foraging. Therefore, we examined pallid sturgeon population characteristics in the Platte River, Nebraska, a large tributary to the Missouri River. We captured 137 pallid sturgeon during 2009-2012. Pallid sturgeon were found throughout the lower 159 km of the Platte River throughout the entire year (March-November); however, pallid sturgeon were more abundant in the lower-most 52 km during the spring and fall seasons. Capture locations were in comparatively deeper water along flow gradients between the thalweg and mid-channel

sandbars. Most pallid sturgeon were of hatchery origin and dispersed an average of 197.5 km (± 26.9 SE) from the original stocking location to the capture site in the Platte River. Although the direct reasons for pallid sturgeon use are unknown, the lower Platte River may be providing habitat or resources that are not typically found in the channelized Missouri River. Continued research in the Platte River and other large tributaries may provide insight for recovery of endemic, large-river species. Persistence of large-river fishes may depend on population connectivity at multiple scales; identifying these connections is critical.

Introduction

Sturgeons (Acipenseridae) have experienced world-wide declines as a result of a combination of anthropogenic effects such as over-harvest, habitat degradation, altered flow regimes, and pollution (Birnstein, 1993). Sturgeons are highly migratory, long-lived, late-maturing fishes that do not spawn annually; a unique combination of traits that make them highly susceptible to human activities (Birnstein, 1993; Birnstein et al., 1997; Pikitch, 2005). Nearly all European and Asian sturgeon species have experienced population declines and have subsequently been classified as either threatened or endangered, and several species will likely become extinct in the near future (e.g. *Acipenser dabryanus*, *Psephurus gladius*; Birnstein, 1993). North American sturgeons have experienced a similar plight in that seven of eight native sturgeon species are listed as endangered, threatened, or of special concern (Williams et al., 1989; Jelks et al., 2008).

Pallid sturgeon *Scaphirhynchus albus* and shovelnose sturgeon *S. platorynchus* are congeners that are found throughout the Mississippi and Missouri river basins. Shovelnose sturgeon is the most abundant and widespread of North American sturgeons;

yet, commercial harvest and habitat degradation have reduced their distribution and abundance (Keenlyne, 1997; Koch and Quist, 2010). Pallid sturgeon are federally listed as endangered (55 FR 36641-36647; U.S. Fish and Wildlife Service, 1990) due to range-wide declines linked to dam construction, commercial harvest, and river modification for navigation (Bailey and Cross, 1954; Birnstein, 1993; Keenlyne, 1997; Mayden and Kuhajda, 1997). A recovery plan was formulated to ensure the remaining wild pallid sturgeon were protected from harm, harassment, or death (Dryer and Sandvol, 1993). A captive broodstock and stocking program was created to augment the declining population and habitat restoration efforts have been initiated (e.g. creation of shallow water habitat and flow modifications).

Pallid sturgeon have been intensively studied in recent years to combat a dwindling adult population that does not support natural recruitment. Much of this effort has occurred in the main-stem Missouri and lower Mississippi rivers. Studies have focused on population attributes, such as population abundance (Braaten et al., 2009; Steffensen et al., 2012; Steffensen et al., 2013a) and dynamics (Keenlyne, 1997; Killgore et al., 2007; Shuman et al., 2011; Steffensen et al., 2010; Steffensen et al., 2013b) to evaluate and monitor the current population. Additional studies have also provided information such as prey selection (Gerrity et al., 2006; Hoover et al., 2007; Grohs et al., 2009; Spindler et al., 2012), habitat use (Bramblett and White, 2001; Hurley et al., 2004; Allen et al., 2007; Phelps et al., 2010), early life-history traits (Kynard et al., 2002; Hrabik et al., 2007; Braaten et al., 2008; Braaten et al., 2009; Phelps et al., 2010; Phelps et al., 2012), and reproductive traits (DeLonay et al., 2009) that will aid future recovery

efforts. There is a breadth of pallid sturgeon research, yet few studies have been conducted in river systems outside of the Missouri and Mississippi rivers.

Tributary streams are important components to main-stem rivers, providing use for fish spawning and reproduction, nursery or refuge habitat, complexity of habitat types, and areas for foraging (Dames et al., 1989; Osborne and Wiley, 1992; Ponton and Copp, 1997; Rice et al., 2001; Pracheil et al., 2009; Neely et al., 2010). Though it is apparent that tributary streams play a functional role in the ecology of large rivers, the importance of tributary streams is not completely understood. Tributary streams disrupt the linear pathway of unidirectional increases in species diversity and nutrient availability by creating discontinuities at tributary confluences (Rice et al., 2001; Kiffney et al., 2006). Confluences provide greater habitat complexity by providing higher substrate heterogeneity, greater stream depth, and increases in wood volume or abundance (Kiffney et al., 2006). Furthermore, tributary streams are often relatively unaltered compared to main-stem rivers and may provide a viable opportunity for conservation of large-river biota (Pracheil et al., 2013).

Little information currently exists on the importance of tributaries for completion of essential life stages for pallid sturgeon. Tributaries may be important for processes such as reproduction and rearing or for habitat types related to refuge and food consumption. For example, pallid and shovelnose sturgeon are known to exist in the lower Yellowstone River, Montana (Bramblett and White, 2001). Pallid sturgeon were found to move into the Yellowstone River during the spring and summer and return to the Missouri River during the fall and winter. Shovelnose sturgeon were ubiquitous users of both the Yellowstone and Missouri rivers; however, movement patterns increased within

the Yellowstone River during the spring. Similarly, telemetry research on pallid sturgeon in the Platte River, Nebraska has indicated increased use (i.e. movements) during the spring and summer periods with migrations to the Missouri River during the fall (Snook et al., 2002; Peters and Parham, 2008). A pallid sturgeon was also assumed to have spawned in the Platte River during the spring of 2012 according to coinciding depth and temperature data recorded on a data storage tag implanted into the fish (DeLonay, USGS, *unpublished data*). These studies have provided valuable seasonal information on *Scaphirhynchus* sturgeon movement and use patterns in tributaries, particularly during the spawning season, but it is largely unknown if tributaries support resident populations and if they do, what role the tributaries might have for long-term sustainability of sturgeon species (i.e. metapopulation dynamics). Therefore, accurate assessments of pallid sturgeon population characteristics in tributary streams will provide critical information that may be beneficial for species recovery. Our objectives were to 1.) determine the distribution and abundance of pallid sturgeon in the lower Platte River, 2.) describe habitat types associated with pallid sturgeon catch, 3.) describe the population stock and age structure, and 4.) examine movement patterns of hatchery-reared pallid sturgeon.

Methods

Study Area

The Platte River basin covers an area of approximately 222,000 km^2 and flows through the Rocky Mountains of Colorado and Wyoming to the high plains of Nebraska

(Crowely, 1983). The Platte River is a highly braided system that forms wide, shallow channels as it crosses the Great Plains. As the Platte River flows across the plains, it cuts away erodible banks and re-deposits fine sand and coarse alluvium (Smith, 1981). The lower Platte River, defined as the lower-most 159 km of river, is free-flowing and has had very few physical anthropogenic alterations (e.g. dams or channelization structures). Although this reach of river appears to have similar historic physical characteristics (i.e. braided channels, erodible banks, and sand bars), it is subject to fluctuations in river discharge (Holland and Peters, 1989). Water usages for hydropower, irrigation, and municipalities creates oscillations in the hydrograph over a variety of temporal scales (e.g. daily and seasonally) (Galat et al., 2005). Our study area was a 159-km reach of the lower Platte River, extending from the confluence of the Loup River Power Canal (near Columbus, Nebraska) to the confluence with the Missouri River. This stretch of river was further divided into two sampling segments to differentiate between hydrologically distinct areas (Fig. 2.1). Segment 1 (river kilometer (rkm) 0-52) has continuous, but variable, flows year round with a significant portion of the base flow coming from the groundwater-fed Elkhorn River (Fig. 2.2) (Galat et al., 2005). Segment 2 (rkm 52-159) also has continuous flow; however, base flows fluctuate daily due to the production of hydroelectricity in the Loup River Power Canal (Holland and Peters, 1989).

Data collection

Pallid sturgeon were collected annually 2009-2012 in the lower Platte River. Fish collection focused on randomly selected reaches within a particular river segment. Specifically, the study area was delineated into 1-km reaches (hereafter referred to as sites) from which fish collection efforts were based. Sample sites were selected using a

stratified random sampling approach where 20 sites were randomly chosen from each segment for each season. Sampling seasons were defined as spring (March-May), summer (June-August), and fall (September-November).

Fish-collection methods followed Peters and Parham (2008) for drifted trammel nets and trotline sampling. Seven trammel nets (i.e. sub-samples) were drifted in habitats where the gear could be properly deployed at each site. Similarly, seven stationary trotlines baited with nightcrawlers *Lumbricus terrestris* were fished at each site overnight. Trammel nets were constructed from monofilament nylon with a depth of 1.8 m and length of 38.1 m. The outside mesh panels were 15.0-cm bar mesh and inside panels were 2.5-cm bar mesh. Trotlines consisted of a 30.5-m main line with 20, 3/0 O'Shaughnessy hooks attached at 1.5-m intervals.

Pallid sturgeon were measured for fork length (mm) and mass (g), and then released. All pallid sturgeon were checked for hatchery markings or tags when collected, and a series of morphometric measurements were taken for species identity corroboration. Recaptured pallid sturgeon provided information relating to year class and time and location of stocking. These data facilitated calculations of age, growth, and movement. In the absence of hatchery tags or markings, a passive integrated transponder (PIT) tag was inserted into the dorsal musculature at the base of the dorsal fin. Tissue samples (caudal fin clip) were collected for DNA analysis to determine the origin of the fish (i.e. hatchery-reared or wild) (Schrey and Heist, 2007; Schrey et al., 2007; DeHaan et al., 2008). Fish that did not match known parental crosses were presumed to be of wild origin.

Catch per unit effort (CPUE) was calculated for trammel nets and trotlines for pallid sturgeon captured in each sampling segment. Trammel net CPUE was reported as the number of fish collected per 100 m drifted and trotline CPUE was reported as the number of fish collected per 20-hook nights.

Size structure and condition of pallid sturgeon were assessed with length frequency histograms and the relative condition factor (LeCren, 1951). Condition was assessed for each of the following length categories described by Shuman et al. (2006): stock-to quality (330-629 mm); quality-to preferred (630-839 mm); preferred to memorable (840-1039 mm); memorable to trophy (1040-1269 mm) and trophy (≥ 1270 mm). Relative condition factor was calculated using the formula:

$$K_n = \left(\frac{W}{W'}\right),$$

where *W* is the observed weight and *W'* is the length-specific mean weight predicted by a weight-length regression equation. The length-weight regression of pallid sturgeon was calculated as:

$$W' = -5.947 + 3.166 * (Log_{10}\, L),$$

where *L* is the fork length of the individual.

Habitat data were collected from about 30% of all sub-samples, chosen randomly, for each site (i.e. 2 of 7 sub-samples), and included water velocity (m^3/s), turbidity (ntu), and conductivity (µS/m). Habitat data were also collected whenever a pallid sturgeon was captured. Other habitat parameters that were collected for every sample, regardless of capture, include water temperature (C°), mean water depth (m), and mean daily

discharge (m^3/s). Comparisons of habitat variables from samples that resulted in the capture of a pallid sturgeon to those that did not were conducted with a two sample *t*-test. All tests were performed in R (R Development Core Team, 2012) and statistical significance was determined at $\alpha = 0.05$.

Results

We captured 137 pallid sturgeon during 2009-2012. Trotlines were more successful at capturing pallid sturgeon and represented 78% (n = 107) of the total catch. Of those captured with trotlines, 85% (n = 91) were sampled during the spring and fall sampling seasons. Trammel nets caught fewer pallid sturgeon and the highest capture frequency with this gear was during the summer (47%, n = 14). Collectively, pallid sturgeon were found throughout the lower Platte River during the entire sampling year (Table 2.1). More than 90% of pallid sturgeon captures occurred in Segment 1 and catch locations were evenly distributed throughout this sampling segment each year (Fig. 2.3). Pallid sturgeon catches were distributed throughout Segment 2, but only 13 individuals were captured.

Most pallid sturgeon from the Platte River were of hatchery-origin (83%, n = 114). Capture of a wild pallid sturgeon was a rare occurrence (n = 7) and most (n = 6) were captured during the 2009 sampling year. However, several other pallid sturgeon (n = 16) could not be identified because either tag information could not be linked to stocking records or tag loss occurred and genetic samples were not collected. Currently, the ratio of wild to hatchery-reared pallid sturgeon in the Platte River is 1:19.5. Nearly

all year classes of pallid sturgeon that have been produced in hatcheries were present in the Platte River and the 2002 year class was sampled in the highest frequency (Fig. 2.4). Hatchery-reared pallid sturgeon ranged in size from 242 mm to 907 mm, whereas wild fish were proportionately larger (729-1045 mm) (Fig. 2.5).

All hatchery reared pallid sturgeon captured in the Platte River were originally stocked at various locations throughout the Missouri River. Stocking information from 89 pallid sturgeon was available and the mean distance moved from the original stocking location to the capture location in the Platte River was 197.5 km (± 26.9 SE) (Fig. 2.6). Most hatchery reared pallid sturgeon collected in the lower Platte River were originally stocked at Bellevue, Nebraska (rkm 967, n = 21) or the confluence of the Platte River (rkm 958, n = 21). However, 10 pallid sturgeon originally stocked at Boonville, Missouri (rkm 314) traveled between 646-736 km to the lower Platte River. Four hatchery-reared individuals were recaptured twice in the Platte River. These fish were at large between 1-3 years from their previous capture in the Platte River and were 12-107 km from the previous encounter.

Catch rates were highly variable, but CPUE was greatest during the 2009 and 2010 sampling years (Fig. 2.7). Catch per unit effort was particularly high in Segment 1 during fall 2009. Higher catch rates also occurred during spring 2009 and 2010, but declined markedly in 2011 and 2012. Catch rates were always low in Segment 2, regardless of season or sampling gear type. An extensive drought occurred in summer 2012 and water levels were significantly reduced throughout the study area, likely impacting catch rates. Trotlines were not deployed during the summer or fall due to low

water and high temperature. Trammel nets were used in both sampling segments during the summer, but were limited to Segment 1 during the fall.

The size structure of pallid sturgeon was truncated toward intermediate and smaller fish (Fig. 2.5). There were no wild pallid sturgeon below 700 mm, indicating a lack of natural recruitment to the population. The length-weight regression provided a good fit to the data (Fig. 2.8). Pallid sturgeon in the Platte River were in excellent condition and met or exceeded values reported from the Missouri River (Table 2.2) (Shuman et al., 2011; Steffensen et al., 2013b).

Pallid sturgeon were captured in a variety of habitat types under varying environmental conditions (Table 2.4). Pallid sturgeon were typically found adjacent to the high velocity of the thalweg in conjunction with slower velocity areas (i.e. pools) created by mid-channel sandbars. However, pallid sturgeon were often found using secondary and braided channels when depth was sufficient (~ 0.5 m). When comparing samples that resulted in a pallid sturgeon capture to those that did not, pallid sturgeon were found more often in deeper water when water temperatures were cooler and turbidity was lower (Table 2.5). All other habitat variables were similar between locations where pallid sturgeon were captured and locations where they were not captured.

Discussion

We employed a standardized, multi-gear sampling approach to describe select pallid sturgeon population characteristics in a large tributary of the Missouri River. Little

was known about pallid sturgeon populations in tributaries such as the Platte River prior to our study. Historical Platte River records indicate that pallid sturgeon were found in the Platte River as far as 52 km upstream from the confluence with the Missouri River. Peters and Parham (2008) captured 15 pallid sturgeon during 2000-2004 and most occurrences were in the spring. Conversely, we found pallid sturgeon residing in the Platte River throughout all sampling seasons in every year. Furthermore, pallid sturgeon were found as far as 159 km upstream; the first documentation of pallid sturgeon above the Elkhorn River confluence. We are aware of few reports of pallid sturgeon captures in tributaries upstream of the lower-most portion of the river (i.e. near the mouth) other than in the lower 114 km of the Yellowstone River (Bramblett and White, 2001) and the entire Atchafalaya River (Keenlyne, 1997). This is likely because little research occurs in tributary systems, particularly in areas upstream from the mouth.

The modern-day Platte River is characterized by high flow variability due to a variety of extrinsic factors such as water withdrawals for irrigation and municipalities and water diversions for the production of hydroelectricity (Holland and Peters, 1989; Galat et al., 2005). These anthropogenic factors create large oscillations in the hydrograph over a variety of temporal scales (i.e. daily, seasonally, etc.) and are likely factors that limit pallid sturgeon occupancy in the Platte River. For example, summer flows are often subjected to extreme (> 1 m) water-level fluctuations from high water demand for irrigation and hydroelectricity (Holland and Peters, 1989; Galat et al., 2005). A low quantity of water coupled with stark fluctuations in diel flow conditions (i.e. hydropeaking) result in previously flowing channels becoming stranded or completely dry. These effects are magnified in areas above the Elkhorn River confluence (i.e.

Segment 2), as substantial water inputs from the Elkhorn River negate stranding and desiccation during normal water years in Segment 1. These hydrologic conditions likely explain the lower abundance of pallid sturgeon in Segment 2 and the overall decrease in abundance observed during the summer months.

Most pallid sturgeon found in the Platte River were of hatchery-origin. Given the high proportion of hatchery-reared pallid sturgeon that were captured, size structure was expected to be dominated by intermediate sized fish (600-800 mm) because hatchery fish have not been in the system long enough to reach greater sizes. No wild pallid sturgeon were captured less than 700 mm, indicating little to no natural recruitment. There was a larger discrepancy in the ratio of hatchery-reared to wild pallid sturgeon (1:19.5) compared to areas of the Missouri River that border the state of Nebraska. Steffensen et al. (2013) reported ratios of 1:3.5 to 1:5.9 throughout 2008-2011. Although the reason for fewer wild pallid sturgeon in the Platte River is unknown, anecdotal evidence suggests that the lack of deep-water habitat (> 1 m) may limit larger, adult pallid sturgeon. Wild pallid sturgeon in the lower Platte River were found in depths $\geq$ 1 m and these depths were often limited both temporally and spatially during our study.

Previous research has indicated that spring is a high-use period in the lower Platte River for pallid sturgeon (Snook et al., 2002; Peters and Parham, 2008). River specialists, such as pallid sturgeon, initiate upstream movements coinciding with peaks in discharge and optimal temperature ranges (DeLonay et al., 2009). After spending a variable amount of time near their apex (presumably spawning), fish move back downstream (Snook et al., 2002; DeLonay et al., 2009). Though previous studies have found pallid sturgeon in the lower Platte River outside of the spawning period, it is often

assumed that the Platte River's ecological relevance is directly related to spawning (Peters and Parham, 2008). Our study provided evidence of year-round use of both wild and hatchery-reared pallid sturgeon in the Platte River. The direct reasons for use are unknown, but the lower Platte River may be providing habitat or resources (e.g. available or abundant prey and refugia) that are not currently found in the Missouri River. Physical characteristics of the lower Platte River are remnant of the historical Missouri River system. For example, emergent sand bars, braided channels, floodplain inundation, and erodible banks were characteristic of the Missouri River prior to reservoir construction and channelization (Hesse et al., 1993; Pegg et al., 2003). Pallid sturgeon evolved a periodic life history strategy (as described in Winemiller and Rose, 1992) to succeed in this type of stochastic environment, therefore, it is likely that the lower Platte River has important ecological aspects that are beneficial for pallid sturgeon survival. At a minimum, the Platte River may simply provide supplemental habitat to the Missouri River.

Recovering and sustaining endangered species is challenging, particularly for fishes that range many kilometers to fulfill life history requirements. Though much has been learned about reproductive characteristics, habitat use, and general population dynamics in at least some portions of their distribution, recruitment bottlenecks for pallid sturgeon are not well understood. Tributary streams have been documented as important sources for both reproduction and recruitment of large riverine species (Robinson and Childs 2001; Pracheil et al., 2009; Neely et al., 2010; Goodman et al., 2012). Furthermore, tributaries are typically less altered than mainstem large rivers, yet provide similar species assemblages in the lower portions of the river (Pracheil et al., 2009;

Pracheil et al., 2013). Thus, tributaries may provide unique opportunities for restoration or conservation efforts aimed at preserving biodiversity of large riverine species (Pracheil et al., 2013). This may be particularly important for pallid sturgeon as the main-stem Missouri River has been altered by dams and channelization, thus creating a fairly homogenous system with relatively uniform depths and velocities (Hesse and Sheets, 1993). Continued research on how the Platte River and other large tributaries may provide benefits and insight for recovery of endemic, large river species is needed. Likewise, understanding the persistence of large-river fishes may depend on understanding population connectivity at multiple spatial and temporal scales given their ability to move great distances.

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Table 2.1. Total number of pallid sturgeon captured during the spring, summer, and fall sampling seasons in Segment 1 (river kilometer – rkm) and Segment 2 of the Platte River, Nebraska during 2009-2012.

Season		Segment 1 (rkm 0-52)	Segment 2 (rkm 52-159)
2009			
	Spring	8	1
	Summer	16	1
	Fall	42	1
2010			
	Spring	21	3
	Summer	1	2
	Fall	12	0
2011			
	Spring	5	2
	Summer	5	0
	Fall	4	1
2012			
	Spring	5	1
	Summer	4	1
	Fall	1	0

Table 2.2. Mean (± SE) relative condition factor (*K*n) of pallid sturgeon captured in the lower Platte River, Nebraska by length categories (Shuman et al. 2006).

Length Categories	N	*K*n
Stock-Quality (330-629 mm)	54	0.99 (0.004)
Quality-Preferred (630-839 mm)	71	0.99 (0.001)
Preferred-Memorable (840-1039 mm)	8	0.97 (0.011)
Memorable-Trophy (1040-1269 mm)	1	0.95
Trophy (> 1269 mm)	0	n/a

Table 2.3. Mean (± SE) and the range (below mean) for habitat variables recorded each time a pallid sturgeon was captured during the spring, summer, and fall sampling seasons in Segments 1 and 2 of the Platte River, Nebraska during 2009-2012.

Parameter	2009	2010	2011	2012
Temperature (°C)	**15.7** (0.8) (3.9-27.7)	**13.5** (0.7) (8.4-27)	**18.7** (2.0) (4-28)	**20.3** (1.5) (12.4-29.4)
Turbidity (NTUs)	**119** (7.8) (41-325)	**138** (13.5) (44-352)	**103** (11.0) (39-176)	**164** (1.5) (55-1000)
Dissolved Oxygen (mg/L)	**7** (0.3) (3-15)	**9** (0.6) (4-17)	**9.5** (0.6) (7-13)	**9** (1.3) (2-15)
Conductivity (µS/cm)	**592** (14.8) (360-890)	**670** (17.4) (435-893)	**644** (21.9) (465-815)	**599** (43.6) (457-925)
Discharge (m^3/sec)	**220** (9.4) (63-343)	**278** (13.7) (117-464)	**278** (13.7) (117-464)	**109** (21.9) (23-229)

Table 2.4. Mean (± SE) values of all habitat parameters measured at gear deployments where pallid sturgeon were captured (present) and those that did not (absent).

Habitat parameter	Present	Absent	Test Statistic
Temperature (˚C)	15.6 (0.6)	19.3 (0.1)	t = -5.91, df =115, $p < 0.001$
Turbidity (ntu)	121.8 (6.9)	143.6 (4.8)	t = -2.60, df =210, $p = 0.010$
Conductivity (µS/m)	624.4 (11.5)	601.6 (4.3)	t = 1.86, df =122, $p = 0.066$
Dissolved oxygen (mg/L)	7.9 (0.3)	7.4 (0.1)	t = 1.28, df =99, $p = 0.205$
Mean daily discharge (m^3/s)	238 (7.4)	226 (1.6)	t = 1.53, df =123, $p = 0.129$
Depth (m)	0.9 (0.03)	0.7 (0.01)	t = 3.30, df =117, $p = 0.001$
Mean column velocity (m^3/s)	0.70 (0.02)	0.73 (0.01)	t = -1.29, df =116, $p = 0.200$

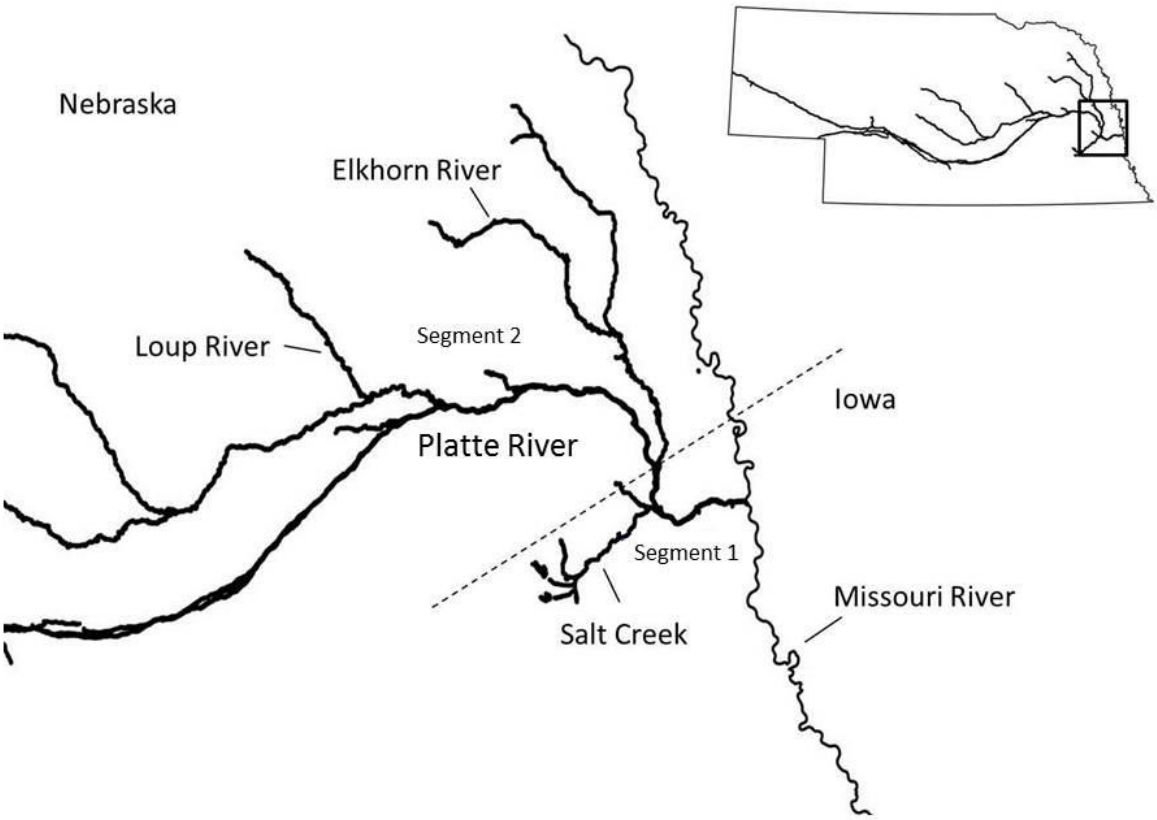

Fig. 2.1. Map of the lower Platte River study area. The dashed line indicates the break between Segment 1 and Segment 2 at the confluence with the Elkhorn River.

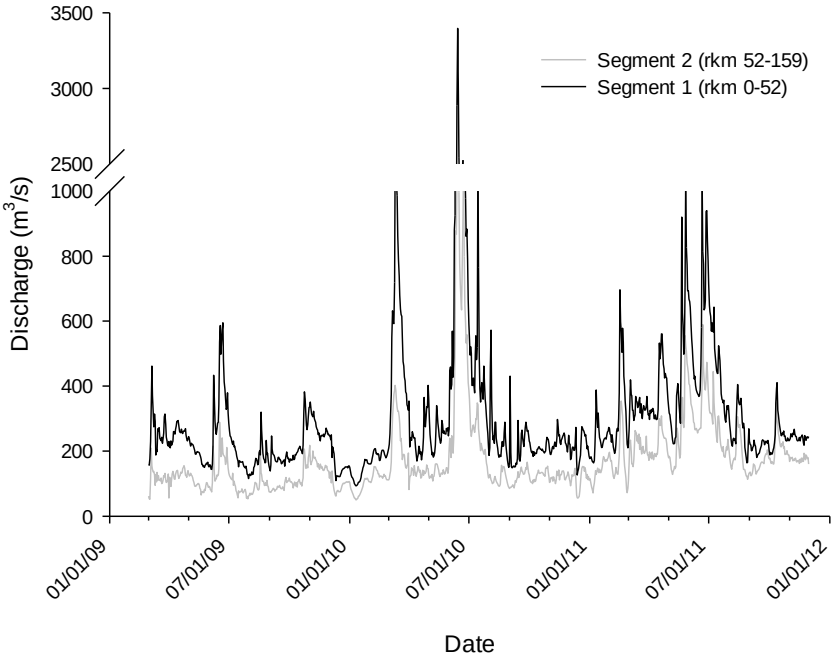

Fig. 2.2. Hydrograph of the lower Platte River, Nebraska throughout the study period (2009-2012). Data from both sampling segments were included to illustrate the differences in hydrology. Data were from USGS gaging stations at Louisville, NE (Segment 1, Gage 06805500) and North Bend, NE (Segment 2, Gage 06796000).

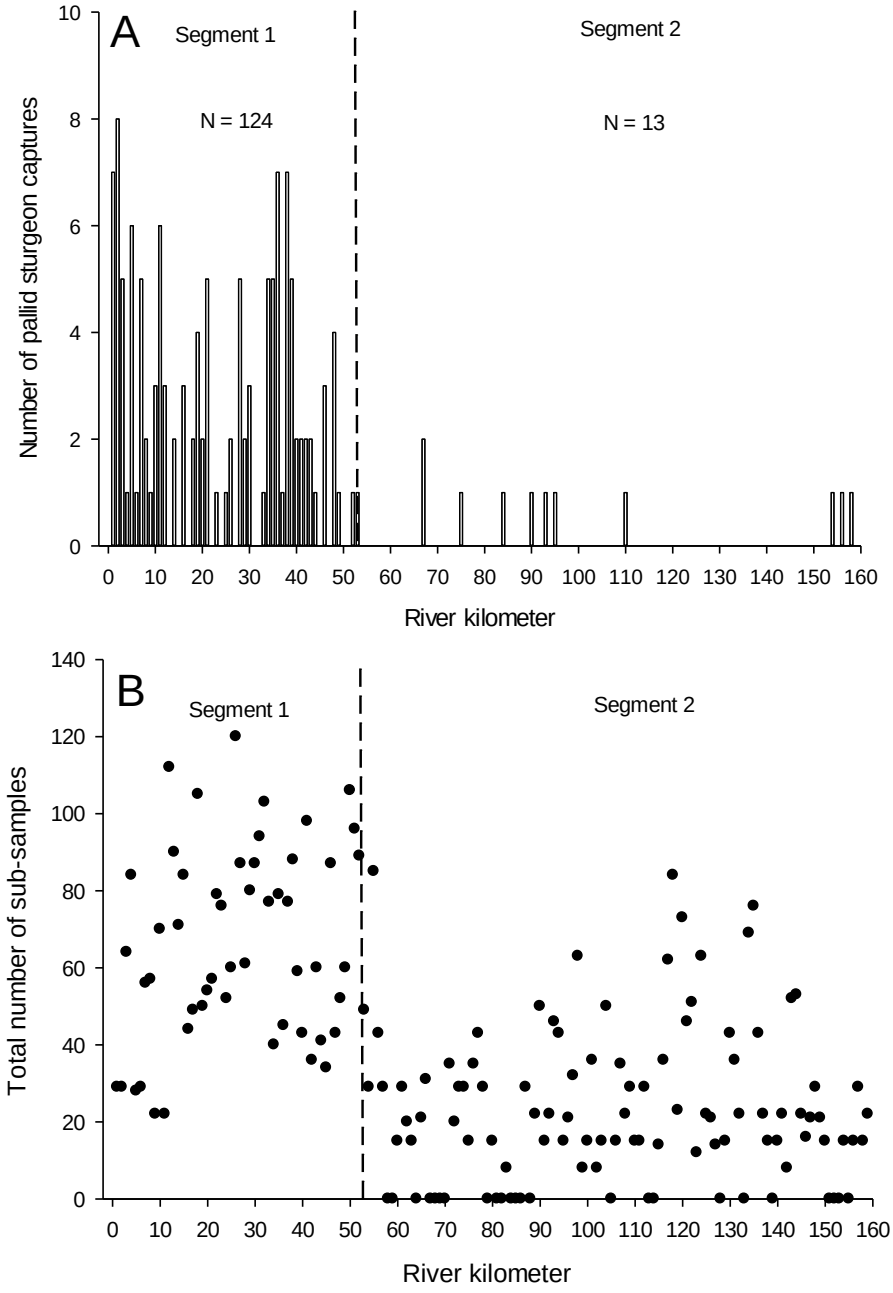

Fig. 2.3. Distribution of pallid sturgeon captures (A) and the total number of sub-samples performed (B) by river kilometer for Segment 1 and Segment 2 of the lower Platte River, Nebraska during the spring, summer, and fall sampling seasons during 2009-2012. The dashed line represents the Elkhorn River confluence, the physiogeographical border between Segment 1 and Segment 2.

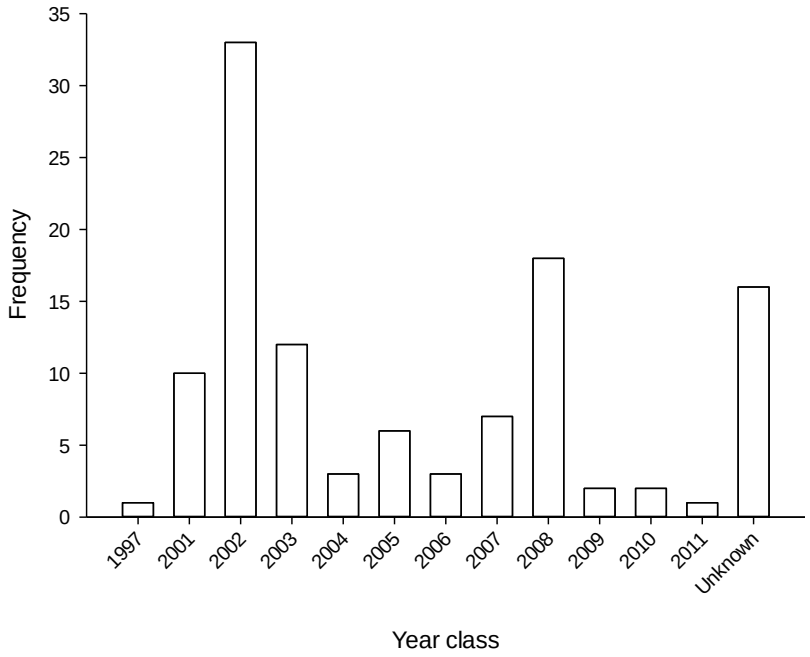

Fig. 2.4. Total number of hatchery-reared pallid sturgeon captured in the lower Platte River, Nebraska for each year class. Also included are hatchery-reared pallid sturgeon that lack information pertaining to birth year (unknown).

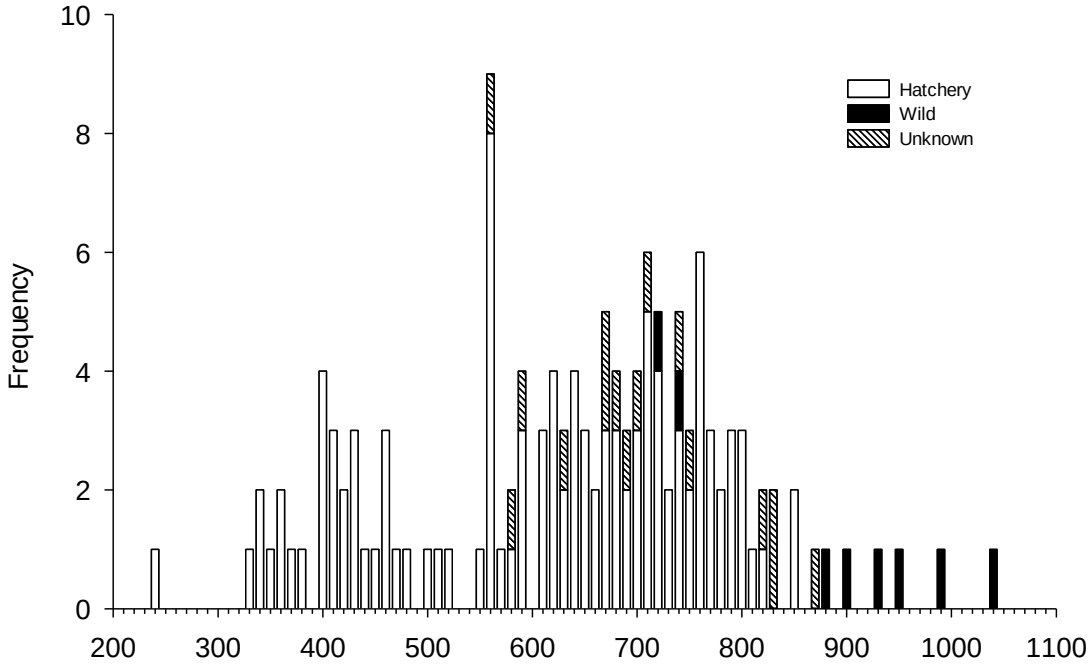

Fig. 2.5. Length frequency distribution of pallid sturgeon captured with both sampling gears for the lower Platte River, Nebraska during 2009-2012.

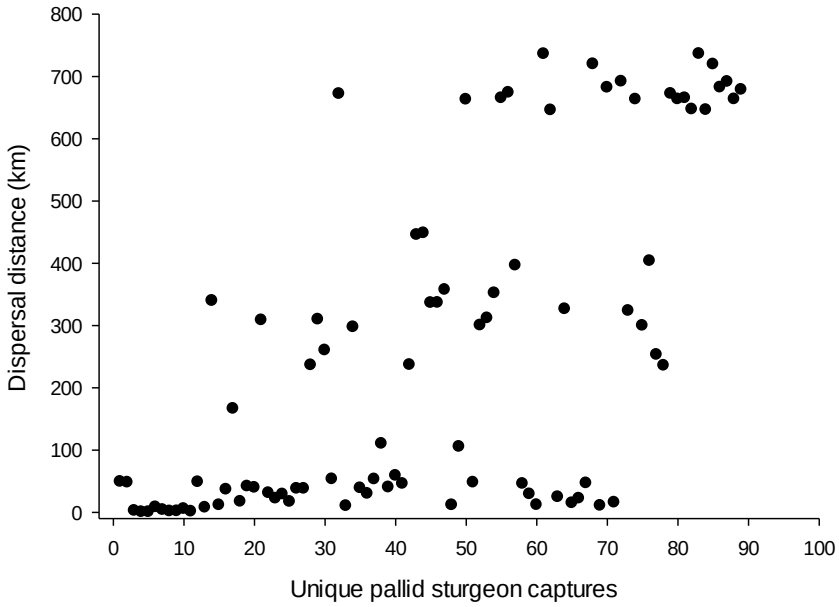

Fig. 2.6. Total dispersal distance (km) from the location at original stocking on the Missouri River to capture in the Platte River. Stocking information was available for 89 hatchery-reared pallid sturgeon.

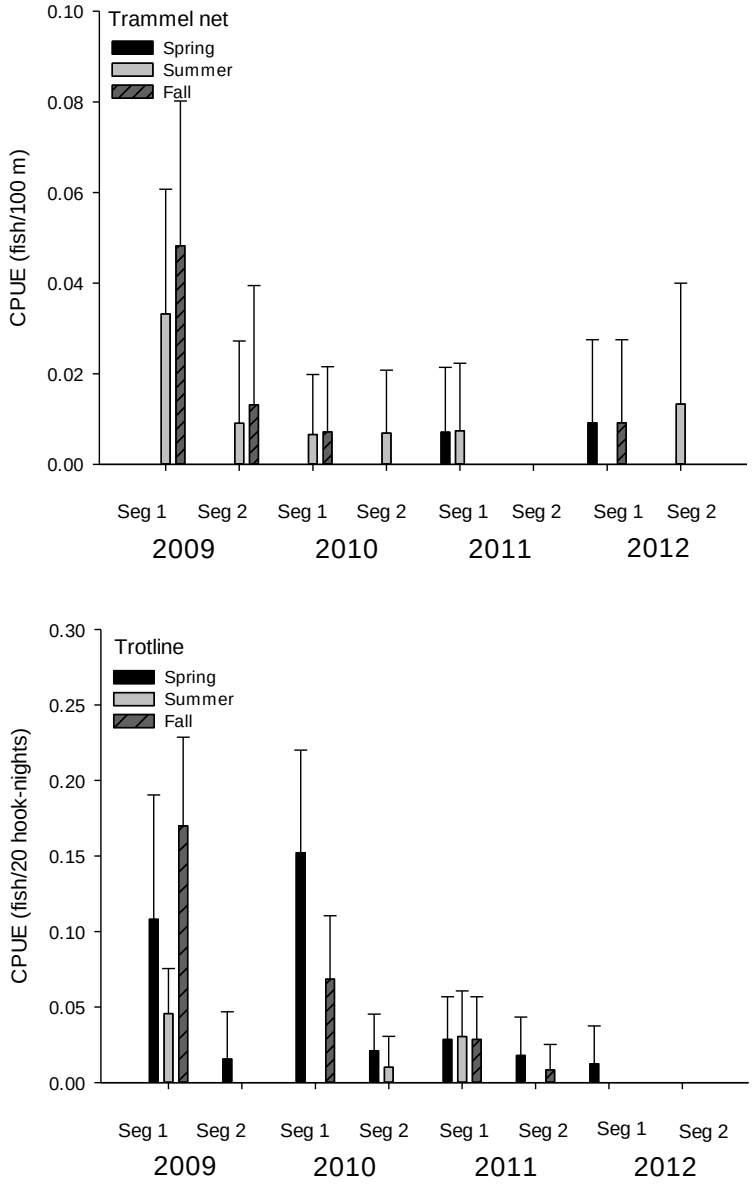

Fig. 2.7. Mean catch per unit effort (CPUE, ± 2 SE) of pallid sturgeon captured with trammel nets and trotlines in Segment 1 (Seg 1) and Segment 2 (Seg 2) of the lower Platte River, Nebraska during the spring (black bars), summer (light grey bars), and fall (dark grey, hatched bars) 2009-2012. No bars represent zero captures of pallid sturgeon, except trotlines were not deployed during the summer and fall of 2012 and trammel nets were not used in Segment 2 during the fall of 2012.

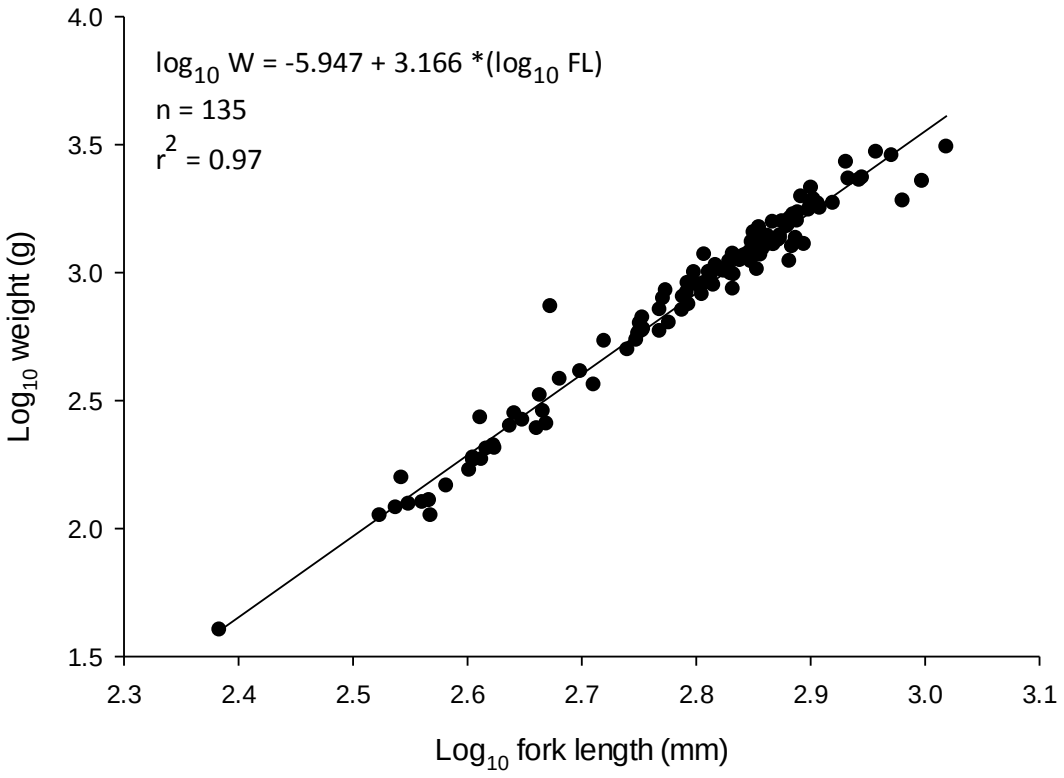

Fig. 2.8. Length-weight relation (log_{10} transformed) for 137 pallid sturgeon captured in the lower Platte River, Nebraska during 2009-2012.

CHAPTER 3: HYDROLOGIC VARIABILITY INFLUENCES DISTRIBUTION AND OCCURRENCE OF PALLID STURGEON IN A MISSOURI RIVER TRIBUTARY

This chapter is prepared for submission to River Research and Applications

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ABSTRACT

A river's flow regime creates and maintains spatial variability in habitat and dictates the distribution and abundance of riverine fishes. Changes to patterns of natural hydrologic variation and disturbance create novel flow conditions and may influence distribution of native fishes. We examined local and regional scale factors that influenced the presence of pallid sturgeon *Scaphirhynchus albus* in the Platte River, a large tributary to the Missouri River in Nebraska, USA. Daily river discharge, diel flow variability, season, and location in the study area were the most supported variables in logistic regression models explaining pallid sturgeon distribution. Probability of pallid sturgeon occurrence was greatest during periods of high discharge (> 90^{th} percentile flows) in the spring and fall. Pallid sturgeon occurrence was always lower when variability in diel flow patterns was high (i.e., hydropeaking). Our results indicate that pallid sturgeon use of the lower Platte River was strongly tied to the flow regime. Therefore, the lower Platte River may provide an opportunity to preserve and restore sturgeon and possibly other large-river fishes through appropriate water management strategies.

INTRODUCTION

A river's flow regime creates and maintains spatial variability in habitat and dictates the distribution and abundance of riverine fishes across a river system (Poff and Allan, 1995; Poff et al., 1997; Pusey et al., 2000; among others). A single river can provide episodic, seasonal, and persistent types of habitat based on the natural variation in frequency, timing, magnitude, duration, and rate of change in seasonal and annual flows (Southwood, 1988; Pegg and Pierce, 2002a; Kennard et al., 2007). Connectivity among habitat types influences local colonization and extinction of fishes across the landscape. The diversity of habitat types created and maintained by hydrologic variability facilitates the distribution of species within a river system by promoting the evolution of physical and behavioral traits used by riverine fishes to carry out specific life history strategies (e.g., reproduction) (Poff and Allan, 1995).

Just as the natural flow regime is directly involved in determining fish assemblages in rivers and streams, temporal patterns in annual flow variability are related to population dynamics, reproduction, and recruitment of native fishes (Bunn and Arthington, 2002). Many characteristics of the life cycle of a particular species of fish are linked to the flow regime. For example, spawning behavior (i.e., reproduction) in some lotic species is triggered by peak discharge events during the spring (DeLonay, 2007; Goodman et al., 2012). During peak flows, lotic species make upstream migrations allowing sufficient distance for larvae to drift back downstream and recruit to the population. Peak flows also allow lateral expansion into the floodplain, providing nursery habitats for young and allochthonous energy inputs for growth and survival (Poff et al., 1997; Bunn and Arthington, 2002; Kennard et al., 2007). Conversely, extended

low flow periods can be important for fishes that are restricted to spawning in the main channel. Concentrated prey is abundant, providing energy for the successful transition from endogenous to exogenous feeding (i.e., 'low flow recruitment hypothesis'; Humphries et al., 1999). Ultimately, a river's natural flow regime, coupled with other environmental conditions (e.g., temperature), creates optimal situations for a variety of life stages or strategies that have adapted to these dynamic environments (Humphries et al., 2013).

Changes to a river's natural flow regime alter the established patterns of natural hydrologic variation and disturbance and creates novel conditions to which native fishes may be poorly adapted (Poff et al., 1997; Malmqvist and Rundle, 2002). Extreme daily variations, such as hydropeaking events produced by power generation, have no natural equivalent and many aquatic populations experience high mortality rates due to stress from wash-out or from being stranded during periods of low flow (Richards et al., 2013). Similarly, streams with low variability in flow have very different fish assemblages than streams with high variability (Meador and Carlisle, 2012). In artificially fluctuating environments, riverine species with specialized adaptations are typically replaced by generalist species that can tolerate frequent and large fluctuations in flow (Poff and Allan, 1995; Poff et al., 1997; Pusey et al., 2000; Pegg and Pierce, 2002b). Many studies have noted shifts in native fish assemblages following modifications to the natural flow regime. Meador and Carlisle (2012) found a greater loss of native species from sites that had reduced natural streamflow variability, and there was a strong relation with the severity of streamflow alterations to the probability of native species impairment. Mims and Olden (2013) examined fish assemblage alterations in response to modified flow

regimes by large dams. Water management operations using dams can create a high degree of flow constancy (i.e., reduced natural variability) and such a change can lead to a shift in life-history strategies. Fish assemblages downstream of dams had a greater proportion of equilibrium species (common in more stable and predictable environments) and a lesser proportion of opportunistic species (common in an environment with unpredictable change) (Mims and Olden, 2013).

Identifying aspects of the flow regime that are conducive or detrimental to native life-history strategies can be an important component for establishing management objectives aimed at enhancing or conserving riverine species (Meador and Carlisle, 2012; Mims and Olden, 2013). However, mainstem large-river systems are permanently altered due to dams and channelization structures, and provide little opportunity for flow manipulation to mimic a pre-modified flow regime. Large tributary streams have a lower degree of physical alteration and may provide an opportunity to enhance conservation of large riverine species, as most large-river species tend to use at least some areas of tributaries as well as mainstems (Neely et al., 2009; Pracheil et al., 2009; Goodman et al., 2012; Pracheil et al. 2013).

Sturgeons and paddlefish (order Acipenseriformes) embody an extant group of obligate-riverine fishes that have been recognized as the most endangered taxon on Earth by the International Union for Conservation of Nature (Lenhardt et al., 2006). Sturgeons represent a lineage dating back to the Lower Jurassic period (200 million years; Pikitch et al., 2005) and have evolved life-history traits and strategies that are well-suited for stochastic riverine environments. The specialized traits (e.g., morphology, long life expectancy, intermittent spawning) that are advantageous for life in variable, yet

predictable, conditions in river systems also make sturgeons highly susceptible to anthropogenic disturbances. Recent work by Goodman et al. (2012) showed a positive relation between discharge and shovelnose sturgeon *Scaphirhynchus platorynchus* spawning in a regulated tributary of the Missouri River. Increased discharge releases from a dam when the temperature regime was suitable for spawning resulted in successful reproduction; whereas, no reproduction was evident in years that lacked a spring pulse (Goodman et al., 2012). An increase in discharge during the spring has been shown to be advantageous for spawning, but how water management throughout the remainder of the year influences the distribution and abundance of sturgeon species that inhabit regulated rivers or their free-flowing tributaries is unknown.

Our goal is to gain an understanding of the effects river regulation has on distribution (i.e., presence) of a large-bodied river specialist, pallid sturgeon *Scaphirhynchus albus*, in an unconstrained tributary of the Missouri River. Pallid sturgeon are an obligate fluvial specialist that are predominantly found throughout the main-stem of the Missouri and Mississippi rivers and portions of several large tributaries. Telemetry studies have shed light on seasonal habitat use of pallid sturgeon and have linked usage to site-specific temperature and flow characteristics (Bramblett and White, 2001; Hurley et al., 2004; Jordan et al., 2006), but the specific environmental conditions (i.e., discharge and temperature regimes) that dictate the presence of river sturgeons are unknown. Thus, the objective of our study was to determine how probabilities of pallid sturgeon captures were influenced by river discharge, variability in daily discharge patterns, and capture-site characteristics (e.g., depth and temperature).

STUDY AREA

The study was conducted on the lower Platte River, Nebraska. The Platte River is a highly braided system that forms wide, shallow channels as it crosses the Great Plains. The lower Platte River, defined as the lower-most 159 km of river, is undammed and has had very few physical anthropogenic alterations (e.g., channelization structures or bank armoring). The lower Platte River has some semblance of its historic characteristics (i.e., braided channels and sand bars), but is subject to severe fluctuations in river discharge (Holland and Peters, 1989). Water withdrawal and diversion for hydropower, irrigation, and municipalities create large oscillations in the hydrograph over a variety of temporal scales (i.e., daily and seasonally) (Galat et al., 2005). The lower Platte River has two hydrologically distinct areas bisected by a large tributary (Elkhorn River) (Figure 3.1). The Platte River below the Elkhorn River confluence (river kilometer – rkm 0-52) is characterized by continuous but variable flows year round with a significant portion of the base flow coming from the groundwater-fed Elkhorn River (Galat et al., 2005). Above the Elkhorn River confluence (rkm 52-159) also has continuous flow; however, diel fluctuations in flow are apparent due to the production of hydroelectricity in the Loup River Power Canal (Figure 3.2).

METHODS

Data collection

Pallid sturgeon were collected during 2009-2011 in the lower Platte River at randomly selected sites (i.e., 1-km reaches) within each river segment. We selected 40

sites from each segment and re-randomized each season. Seasons were delineated as spring (March- May), summer (June-August), and fall (September-November). Fish collection methods followed Peters and Parham (2008) and Drobish (2007) for drifted trammel nets and trotline sampling. Seven trammel nets (i.e., sub-samples) were drifted in suitable habitat (i.e., where gear could properly be deployed) at each site. Similarly, seven stationary trotlines baited with nightcrawlers *Lumbricus terrestris* were fished at each site overnight. Trammel nets were constructed from monofilament nylon with a depth of 1.8 m and length of 38.1 m. The outside mesh panels were 15.0-cm bar mesh and inside panels were 2.5-cm bar mesh. Trotlines consisted of a 30.5-m main line with 20, 3/0 O'Shaughnessy hooks attached at 1.5-m intervals.

Water temperature (C°) and mean water depth (m) were recorded for every sub-sample. Additional habitat data were collected from 30% of all sub-samples, selected at random, for each site (i.e., 2 of 7 sub-samples). Variables used to describe these local scale habitat parameters include mean water column velocity (m^3/sec), turbidity (ntu), and conductivity (μS/m). These parameters were also recorded whenever a pallid sturgeon was captured. We used daily discharge data from the United States Geological Survey (USGS) at North Bend, Nebraska (above the Elkhorn River confluence; Gage 0679600) and Louisville, Nebraska (below the Elkhorn River confluence; Gage 06805500) to describe regional scale factors that might influence pallid sturgeon occurrence. Sub-daily flow data (i.e., 15-min readings) were used to calculate a coefficient of diel variation to depict the diel variation in discharge.

Data analyses

We fit generalized linear models (GLMs) to our binomial capture data (0 = failure, 1 = success) using a logit link function (R Development Core Team, 2012). We used site-specific habitat parameters and river discharge characteristics from the nearest USGS gaging station to predict the probability of pallid sturgeon occurrence. Continuous variables included mean daily discharge, coefficient of diel variation (CV), river kilometer, temperature, turbidity, and mean water column velocity. The effect of sampling seasons was treated as a categorical variable. We constructed 22 *a priori* candidate models (Table 1) and used an information theoretic approach (Akaike's Information Criterion [AIC]) to rank candidate models and to account for the model uncertainty. The candidate model with the lowest AIC was selected as the best model. To rank the remaining models, we calculated the ΔAIC value where the difference of the best model AIC score and the AIC of the remaining models was: $\Delta i = (\mathrm{AIC}_i - \mathrm{AIC}_{min})$. Akaike weights ($w_i$) were computed for each model to help gauge the relative support for each model among the model set (Burnham and Anderson, 2002).

RESULTS

We captured 125 pallid sturgeon in 4,695 sampling gear deployments during 2009-2011. Pallid sturgeon were captured throughout a wide range of habitats and were found throughout the entire study area during all sampling seasons. However, pallid sturgeon were observed in higher frequency in locations below the Elkhorn River confluence (Figure 3.3) and during the spring (n = 46) and fall (n = 61) sampling seasons.

A model that contained the effects of sampling season, river discharge, and location in the study area (rkm) was the best candidate model, having a weight of 0.47

(Table 3.1). There was a longitudinal effect of the probability of pallid sturgeon occurrence, with the highest probability occurring near the mouth of the river and a decreasing probability of occurrence moving upstream (RKM: -0.02 ± 0.004). Inclusion of the CV parameter into the top model accounted for 25% of the remaining weight (Table 3.1). The remaining model that carried a substantial portion of the total weight (23 %) was a less parsimonious variation of these two models, with a three-way interaction between season, river discharge, and CV. We chose not to model-average our predictions due to the cumulative weights of these similarly constructed models (Burnham and Anderson, 2002).

We used our top two parsimonious models to make inferences on probabilities of pallid sturgeon occurrence in the lower Platte River. We evaluated the effects of low, medium, and high discharge values (i.e., 10^{th}, median, and 90^{th} percentile) for each sampling season to assess how probabilities of pallid sturgeon occurrence changed throughout the lower Platte River under differing flow conditions. Our first model predicted that the greatest probability of pallid sturgeon occurrence during the spring and fall occurred under a high discharge regime (i.e., 90^{th} percentile in flows) (Table 3.2). This was particularly true during the fall when the highest overall probability of pallid sturgeon occurrence was observed (Figure 3.4). Occurrence of pallid sturgeon during the summer was greatest under periods of low flow. Using our second model, we examined how low and high diel flow variability (i.e., 10^{th} and 90^{th} percentile in CV) influenced pallid sturgeon occurrence under all three discharge regimes in each sampling season. A low CV always predicted a higher probability of pallid sturgeon occurrence, regardless of discharge level or sampling season (Figure 3.5).

DISCUSSION

Pallid sturgeon were captured throughout the entire study reach of the lower Platte River (159 km) and were found throughout all three seasons annually. This was not expected because it was previously unknown if large riverine specialists, such as pallid sturgeon, use the entire lower Platte River outside of the spawning season. The Platte River tributary is clearly an important component to the metapopulation of pallid sturgeon as fish occupied habitat patches throughout the year, particularly during the fall sampling period. In addition, pallid sturgeon were collected in the upstream reaches (rkm 52-159) where they have not been documented. This wide distribution of pallid sturgeon occurrence provides additional evidence for the importance of the Platte River tributary outside of the lower portions of the river that are heavily influenced by the confluence with the Missouri River.

Factors that were responsible for the distribution of pallid sturgeon in the Platte River were best explained by regional scale factors associated with the flow regime. An interaction between river discharge during each of the three sampling seasons as well as the diel variation in flow was the best predictors for pallid sturgeon occurrence. Our model predicted the highest probability of pallid sturgeon occurrence under high discharge regimes. For modeling purposes, we used the 90^{th} percentile of the observed mean daily discharge values for all sampling occasions (518 m^3/s) as the representative value for the high discharge classification. Discharge values near this range of flows are infrequent in the lower Platte River and usually are associated with high precipitation events. Though it may not be feasible to allocate water for consistent flows of this

magnitude at will, these results provide important information for future water management during years of above normal snow-melt or precipitation (e.g., environmental flow assessment).

There was a negative relation between high variability in daily flows and pallid sturgeon occurrence during the spring and fall. Diel flow variation in the lower Platte River is a result of hydropeaking from a nearby power facility on the Loup River, a tributary to the Platte River (Figure 1). Water from the Loup River is diverted through a series of canals to the hydroelectric facility. After generating power, water is re-directed to the Platte River just downstream of the Loup River confluence. More water is used during periods of peak electricity usage, thereby creating large (> 1 m) diel oscillations of water returns. These effects are exacerbated in the upper 107 km of the lower Platte River because very little base flow comes from the central Platte River due to water withdrawals for irrigation (Galat et al. 2005). These large oscillations in the hydrograph create drastic changes in river stage level and many of the braided channels within the river are often stranded or completely desiccated during low flow periods. Though the effects of hydropeaking are detectable in the hydrograph of the lower 52 km of the Platte River, substantial water inputs from the Elkhorn River buffers the magnitude of diel change, thereby, negating stranding and desiccation during normal water years. This is likely the reason why the CV was not included in the top model from our results because CV is only a good predictor of pallid sturgeon presence where hydropeaking occurs.

The probability of pallid sturgeon occurrence declined longitudinally from the mouth of the Platte River to the upstream-most sampling site for all of our predictions. This precipitous decline beyond the confluence of the Elkhorn River (rkm 52) illustrates

the affect reductions in quantity of water and diel fluctuations in flow can have on large-bodied riverine species. Many authors have shown that extremes in river flow and the patterns of flow variability directly affect the local community structure (Poff and Allan, 1995; Pusey et al., 2000; Biggs et al., 2005; Kennard et al., 2007; and others). Poff and Allan (1995) showed that streams with high flow variability had fish assemblages that were more characteristic of small streams and lentic systems that consisted of proportionately fewer medium to large-bodied river species. In streams with excessive variability, specialization of traits is unlikely to occur and generalism is typically observed as the most successful strategy (Pusey et al., 2000; Mims and Olden, 2012). Therefore, reducing diel fluctuations in flow and water withdrawals for various purposes would likely increase the number of pallid sturgeon occurrences in areas above the Elkhorn River confluence.

Previous work has indicated that spring is a high-use period in the lower Platte River for lotic species (Snook et al., 2002; Peters and Parham, 2008; Neely et al., 2009). River specialist such as pallid sturgeon and blue sucker *Cycleptus elongatus* initiate upstream movements coinciding with peaks in discharge and optimal temperature ranges. After spending a variable amount of time near their apex, most fishes move back downstream (Snook et al., 2002; Neely et al., 2009). Though large-bodied lotic species have been found in the lower Platte River outside of the spawning period, it is often assumed that the Platte River's ecological relevance is directly related to spawning (Peters and Parham, 2008). Our results show that the probability of pallid sturgeon occurrence was greatest during the fall sampling period and occurrence was particularly high during periods of high discharge. Though the direct reasons for use are unknown,

the lower Platte River may be providing habitats or resources that are not typically found in the Missouri River such as emergent sand bars and braided channels, available or abundant prey, and refuge from high velocities.

Pallid sturgeon captures were low during the summer sampling period, regardless of environmental conditions. Contrary to expected results, our model predicted that the probability of pallid sturgeon occurrence during summer was highest under a low flow regime. As previously described, summer flows are often low due to high water demand coupled with low precipitation. It is unknown how sampling gear efficiencies are influenced by low flow. Summer flows also may congregate pallid sturgeon and our site selection may have precluded us from collecting them. Future research to describe seasonal influences on catchability and summer use in the Platte River is needed.

Preserving or enhancing biodiversity of lotic species is challenging in that few free-flowing, large (> 350 m^3/s) river systems exist throughout much of the northern third of the world (Dynesius and Nilsson, 1994). Anthropogenic effects such as fragmentation by dams, water regulation from reservoir operations, and water diversion and irrigation withdrawals have been linked to losses in biodiversity (Malmqvist and Rundle, 2002). Although the lower Platte River is subject to flow management from several water constituents, few physical alterations (i.e., dams and water control structures) have occurred resulting in a system that retains many of the historical characteristics such as shifting sandbars, braided channels, and connectivity to the floodplain, but is subject to water management issues. Therefore, the lower Platte River provides an opportunity to preserve and enhance ecological processes in a system that could be optimally managed

to accommodate appropriate water management that emulates key elements of the natural flow regime.

Management of lotic systems will continue to be a difficult task as water managers are challenged to meet the needs of supplying suitable drinking water, irrigation, recreation, and hydro-electricity production, while not degrading or disrupting freshwater ecosystems. Establishing environmental flows (Tharme, 2003; Arthington et al., 2006) has been used as an alternative to minimum flow thresholds by accounting for ecosystem processes while achieving sustainable water-resource management (Bobbi et al., 2013). Environmental-flow assessments attempt to maintain freshwater biodiversity by identifying and conserving influential components of the natural flow regime (Poff et al., 1997) while accounting for water allocation for other water users (Lind et al., 2007). Future research is needed for developing a collaborative and adaptive approach for managing water to meet ecological and societal demands in lotic systems like the Platte River.

The role of tributary streams has gained recent attention for conservation of aquatic biodiversity (Kiffney et al., 2006; Sarkar et al., 2010; Pracheil et al., 2013). Tributaries typically are physically altered to a lesser degree and provide similar species assemblages in the lower portions of the river compared to main-stems (Pracheil et al., 2009; Pracheil et al., 2013). Thus, tributaries may provide unique opportunities for restoration or conservation efforts aimed at preserving biodiversity of large riverine species (Pracheil et al., 2013). This may be particularly important for pallid sturgeon as the main-stem Missouri River has been permanently altered by dams and channelization, creating a fairly homogenous system with relatively uniform depths and velocities (Hesse

and Sheets, 1993). Continued research in the Platte River and other large tributaries may provide insight into the importance of population connectivity at multiple scales for species persistence.

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Table 3.1. Candidate models, Akaike's Information Criterion (AIC), number of parameters (k), increase over the lowest AIC (Δ AIC), and Akaiki model weight (wi) for models we used to predict the occurrence of pallid sturgeon throughout the lower Platte River during 2009-2011.

Candidate Models	AIC	*k*	Δ AIC	*w*
presence ~ SEA*DISC + RKM	-4138.05	8	0.00	0.47
presence ~ SEA*DISC + CV + RKM	-4136.79	9	1.26	0.25
presence ~ SEA*DISC*CV + RKM	-4136.58	14	1.47	0.23
presence ~ SEA*DISC + CV	-4133.58	8	4.46	0.05
presence ~ SEA*DISC	-4118.53	7	19.52	0
presence ~ SEA*CV + RKM	-4114.84	8	23.20	0
presence ~ SEA*CV + DISC + RKM	-4113.13	9	24.92	0
presence ~ SEA*CV + DISC	-4104.55	8	33.50	0
presence ~ SEA*CV	-4104.08	7	33.97	0
presence ~ RKM*CV	-4098.30	5	39.75	0
presence ~ RKM	-4094.76	3	43.29	0
presence ~ DISC*CV + RKM	-4094.56	6	43.49	0
presence ~ RKM*DISC	-4093.22	5	44.83	0
presence ~ DISC*CV + SEA	-4092.37	7	45.68	0
presence ~ DISC*CV	-4084.45	5	53.60	0
presence ~ CV	-4081.41	3	56.64	0
presence ~ YEAR	-4071.06	4	66.99	0
presence ~ SEA	-4051.58	4	86.47	0
presence ~ RKM*CV + TEMP	-3783.41	6	354.64	0
presence ~ TEMP	-3724.23	3	413.82	0
presence ~ SEA*RKM*CV + TEMP + TURB + VEL	241.29	16	4379.34	0
presence ~ VEL	322.09	3	4460.14	0
presence ~ TURB	327.72	3	4465.77	0

SEA, Sampling season; DISC, Mean daily discharge (m^3/sec); CV, Coefficient of diel variation; RKM, River kilometer; TEMP, Temperature (˚C); TURB, Turbidity (ntu); VEL, Mean column velocity (ft3/sec).

Table 3.2. Probability of pallid sturgeon occurrence at varying levels of discharge during the spring, summer, and fall seasons. Probabilities were generated for four evenly spaced locations throughout the lower Platte River.

		River kilometer (RKM)			
Season	Discharge percentiles	RKM 1	RKM 52	RKM 105	RKM 159
Spring	10th percentile	0.054	0.020	0.007	0.002
	Median	0.062	0.023	0.008	0.003
	90th percentile	0.098	0.038	0.013	0.005
Summer	10th percentile	0.049	0.018	0.006	0.002
	Median	0.039	0.014	0.005	0.002
	90th percentile	0.017	0.006	0.002	0.001
Fall	10th percentile	0.040	0.015	0.002	0.002
	Median	0.077	0.029	0.005	0.003
	90th percentile	0.456	0.231	0.011	0.034

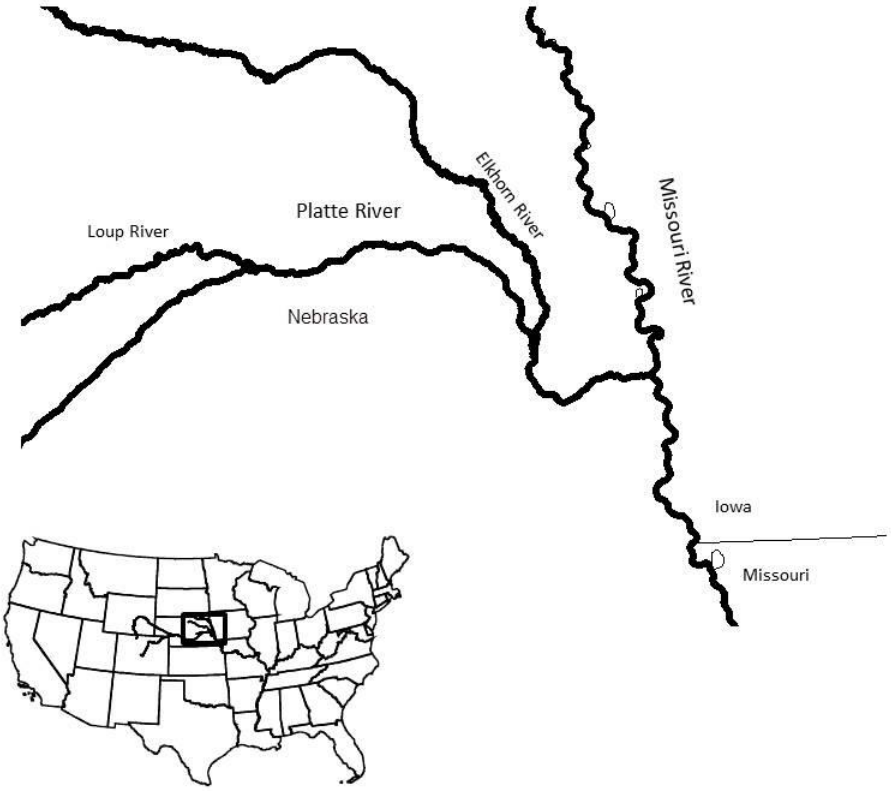

Figure 3.1. Map of the lower Platte River study area.

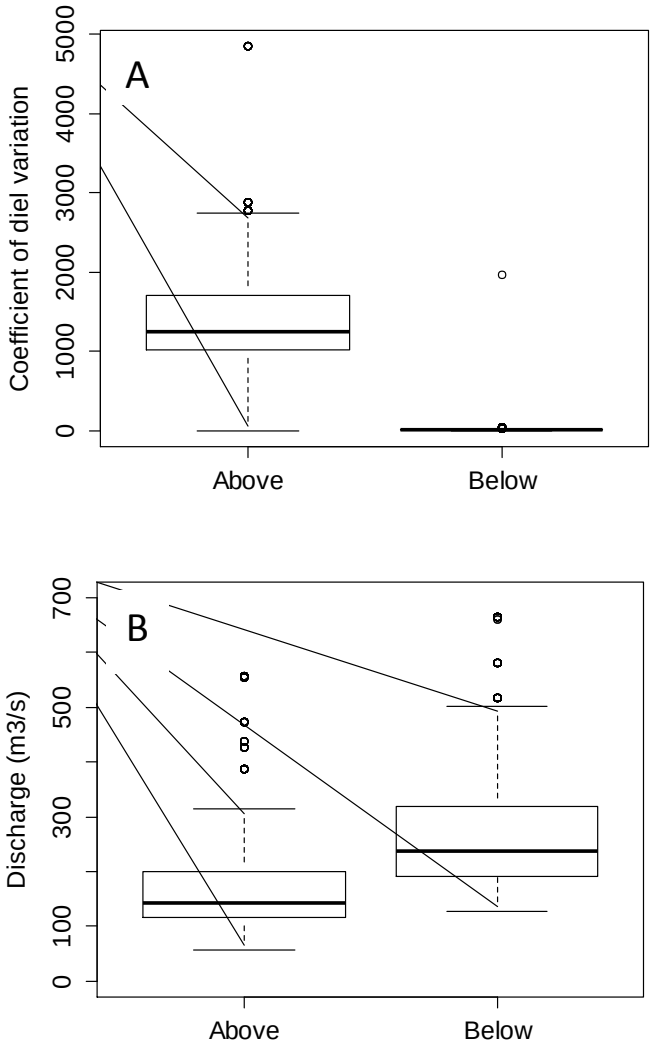

Figure 3.2. Coefficient of diel variation (A) and mean daily discharge (B) for areas above and below the Elkhorn River confluence in the lower Platte River, Nebraska. Discharge data were recorded from USGS gaging stations at Louisville, NE (Gage 06805500) and North Bend, NE (Gage 06796000). The horizontal line of the box plot is the median, the ends of the box are the upper and lower quartiles, and the vertical lines are the full range of values in the data excluding outliers (i.e., circles).

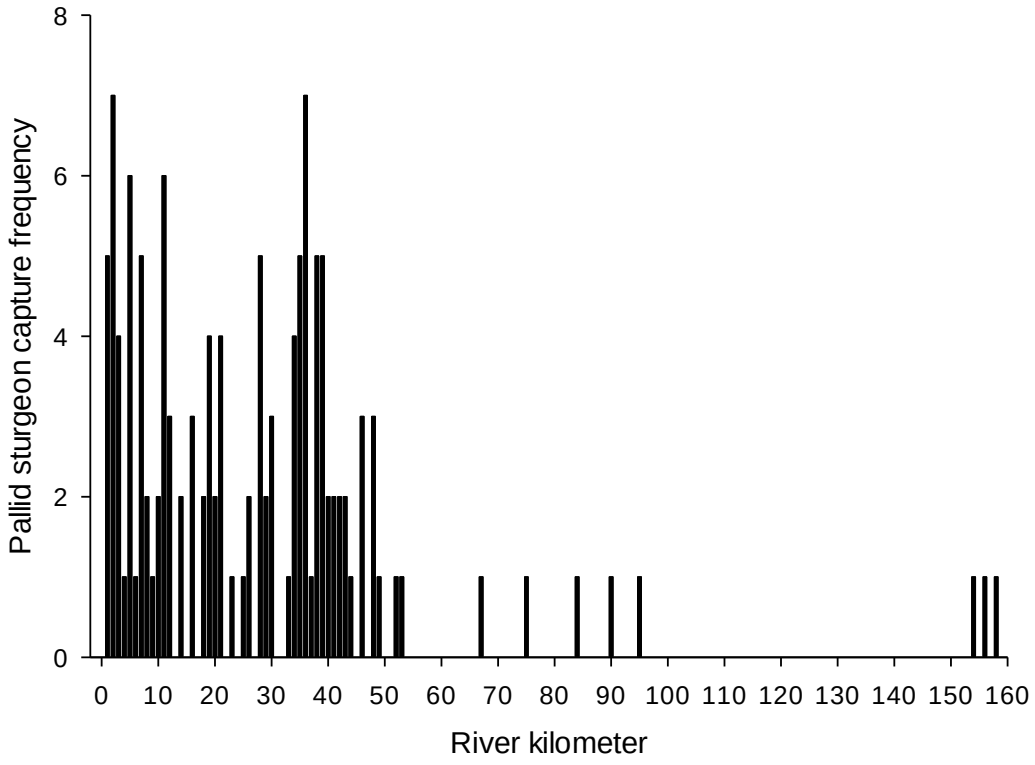

Figure 3.3. Distribution of pallid sturgeon captures by river kilometer in randomly selected sites of the Platte River, Nebraska during the spring, summer, and fall sampling season in 2009-2011.

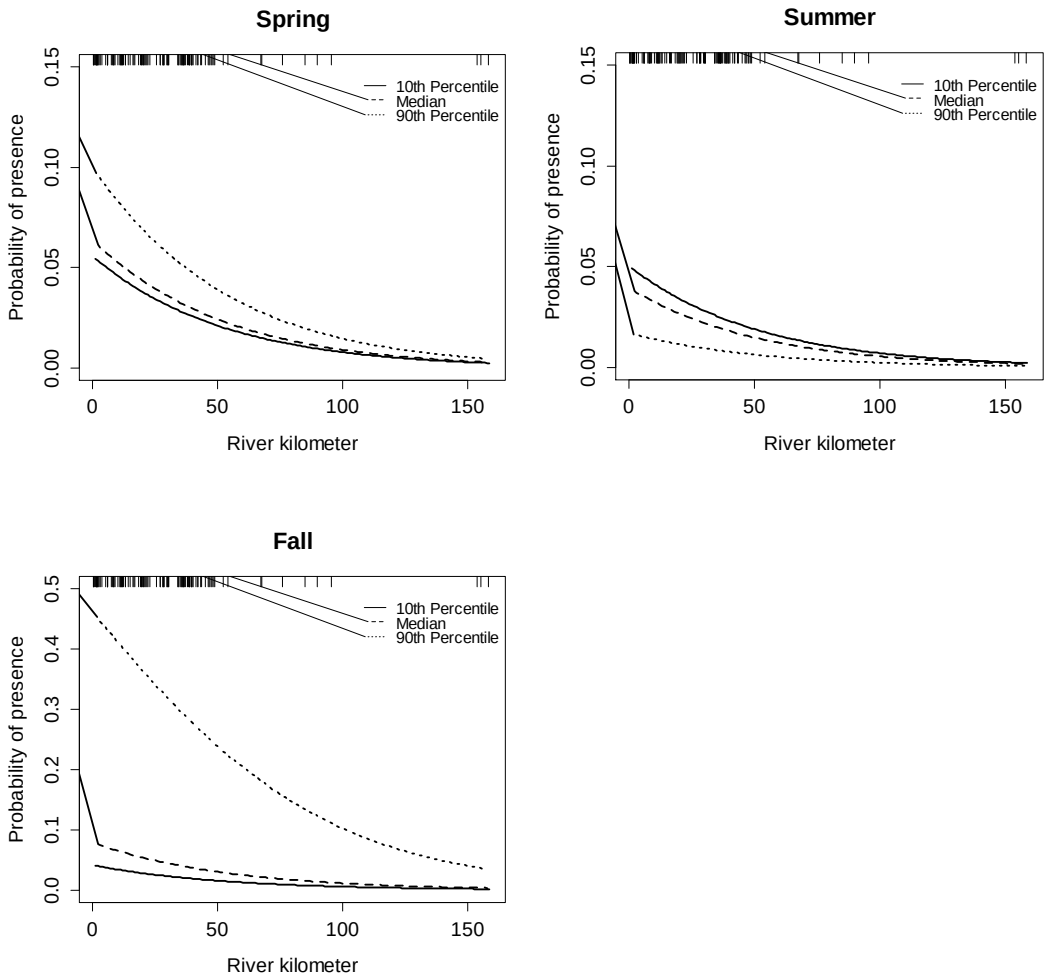

Figure 3.4. Predictive curves for the probability of pallid sturgeon occurrence throughout the lower Platte River (rkm 0-159) under the 10th (108 m^3/s), median (202 m^3/s), and 90th percentiles (379 m^3/s) of the reported mean daily discharge for each sampling event (day). Tick marks at the top of each box represent actual locations of pallid sturgeon captures from 2009-2011.

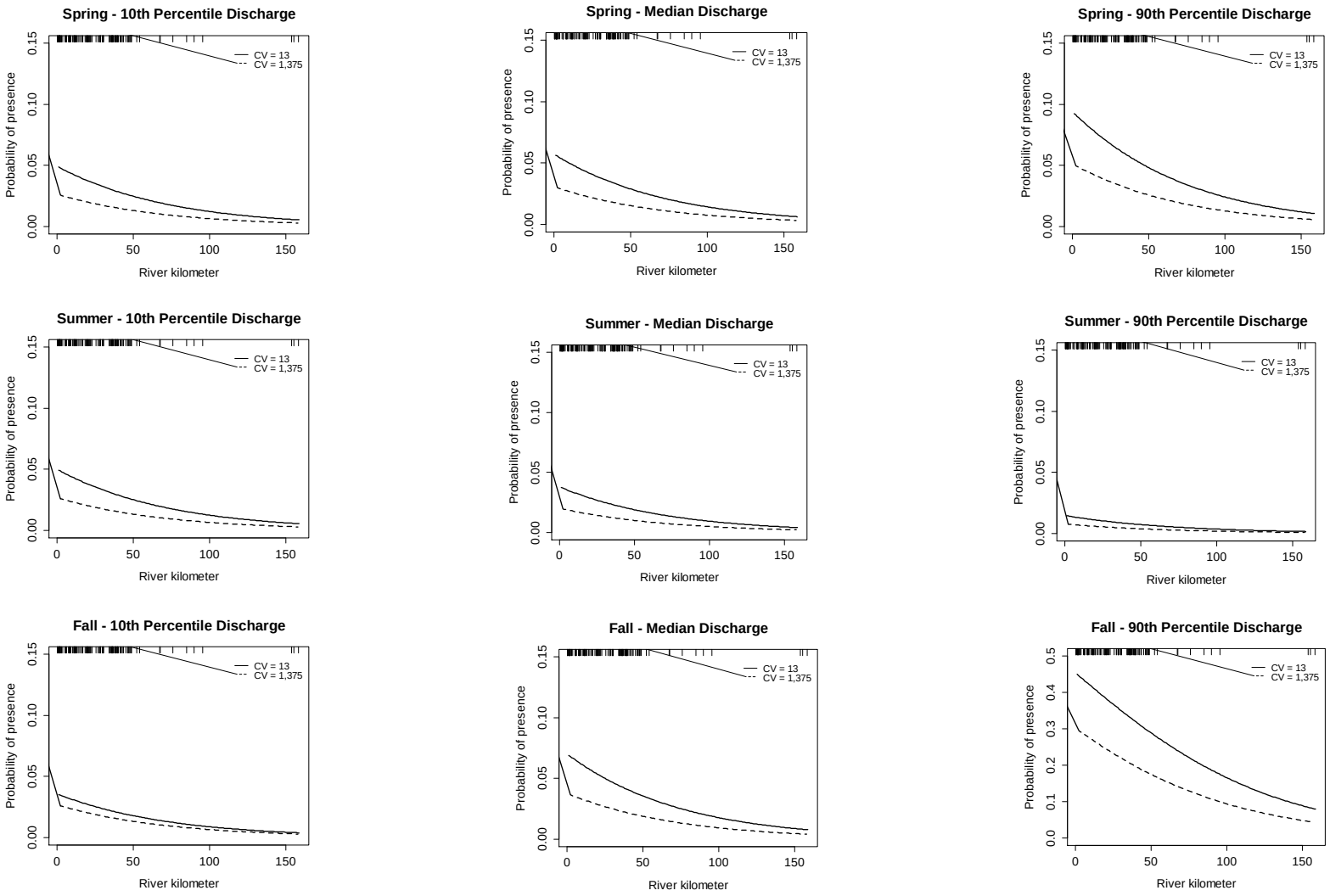

Figure 3.5. Predictive curves for the probability of pallid sturgeon occurrence throughout the lower Platte River (rkm 0-159) under the 10th (CV = 13) and 90th (CV = 1,375) percentile of the coefficient of diel variation for varying discharge regimes each sampling season. Tick marks represent actual pallid sturgeon captures from 2009-2011.

CHAPTER 4: IS THAT YOUR FINAL ANSWER? USING MARK-RECAPTURE INFORMATION TO VALIDATE AND ASSESS AGE AND GROWTH OF LONG-LIVED SPECIES

This chapter is currently under review with the Canadian Journal of Fisheries and Aquatic Sciences

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Abstract

Long-lived species from marine and freshwater environments have experienced declines linked to anthropogenic effects such as over-exploitation, dam construction, and habitat modification. An understanding of the age-structure and the associated dynamics (i.e., growth and mortality) determined from these data for long-lived species is critical for both perseverance of at-risk species and maintenance of exploited species. We used long-lived pallid sturgeon *Scaphirhynchus albus* to evaluate the efficacy of mark-recapture data from known-age, hatchery-reared pallid sturgeon to validate age estimates and corroborate growth estimates generated from back-calculations obtained from sectioned pectoral fin rays. Accuracy of fin ray age estimates from known-age fish was 13%; whereas 72% of estimates were within two years of the true age. Back-calculated lengths were estimated with and without prior knowledge of age and compared to mark-recapture data. Annual growth was significantly different between back-calculation

procedures and actual observations of tagged pallid sturgeon. Even with prior knowledge of age, growth trajectories did not resemble patterns observed in mark-recapture data. Age for pallid sturgeon of any given size was estimated with parameters derived from mark-recapture data and the predicted length-at-age relation was similar to observations from known individuals. We recommend researchers understand the potential bias from age structures of long-lived species before adhering to conventional, calcified structure methods that have previously been conducted or are easier to calculate. In instances where age determination for all ages of interest cannot be verified, mark-recapture appears to be a viable solution for examining growth and has shown promise as a tool for estimating ages in long-lived species with calcified structures that are difficult to read.

Introduction

Long-lived fish species (> 20 years) pose a unique set of challenges for assessment and monitoring as population-level responses may take years to be realized. In marine fisheries, long-lived species are often targeted for commercial harvest (Trippel 1995; Hutchings and Reynolds 2004). Over-exploitation of many fish stocks has resulted in a collapse of the fishery. Complete fishing closures, although unlikely given the current socio-political situation, may be the only means to restore abundance to previous levels (Pauly et al. 2002; Hutchings and Reynolds 2004). Furthermore, many long-lived fish species such as those that live in or near coral reefs have exhibited declines due to destruction of habitat (Coleman et al. 2000; Hughes et al. 2003; Bellwood et al. 2004). Long-lived fishes from freshwater systems are not exempt to excessive exploitation, but have also been subject to intense anthropogenic effects such as dam construction,

pollution, and habitat modifications that have further hindered population stability (Birstein et al. 1997; Boreman 1997; Dudgeon et al. 2006; Leveque et al. 2008). Many long-lived species have adapted a periodic life-history strategy where longevity compensates for variation in juvenile survival and environmental influence on reproductive success (Winemiller 2005). Sporadic recruitment patterns limit these species' ability to increase population size quickly, making long-lived species highly susceptible to declines in abundance (i.e., anthropogenic effects). Therefore, an understanding of the age-structure and the interacting dynamics (i.e., growth and mortality) of long-lived species is critical for both perseverance of at-risk species and maintenance of exploited species.

Several long-lived species inhabit freshwaters of North America and most inhabit large rivers. Fishes such as sturgeon (Genus: *Acipenser* and *Scaphirhynchus*), paddlefish (*Polyodon spathula*), alligator gar (*Atractosteus spatula*), and several large species from families Catostomidae and Cyprinidae have been known to live greater than 30 years (Scoppettone 1988; Bemis et al. 1997; Pikitch et al. 2005; Buckmeier et al. 2012). These long-lived species, particularly sturgeons and paddlefish, have received considerable attention in recent years due to range-wide declines linked to anthropogenic effects such as over-harvest, dam construction, and loss of habitat (Boreman 1997). Determining the age structure has been, and will continue to be, an integral component for assessment of these long-lived species so that demographic models used to predict population viability and responses to management actions can be assessed (Bajer and Wildhaber 2007; Koch et al. 2009; Jager et al. 2010; Steffensen et al. 2013. Age of fishes is typically determined by observing periodic growth increments that are produced in calcified structures. If

growth marks are formed consistently and can be interpreted accurately, an estimate of age is produced (Campana and Neilson 1985). Similarly, the distance between growth marks relative to the size of the calcified structure can often be correlated to annual, somatic growth in the fish (Francis 1990). These procedures are based on assumptions of consistent deposition of growth marks and that the distance between marks are in direct proportion to the somatic growth of the fish. However, validation of these techniques is an often overlooked prerequisite before using age data for analyses. Validation for individual species should include a verification of growth increment periodicity across the entire age range of interest, particularly for long-lived species (Beamish and McFarlane 1983; Campana 2001). Failure to properly verify absolute age estimates can have drastic effects, such as providing overly optimistic or pessimistic growth and mortality estimates. Campana (2001) reported several examples of long-lived species (i.e., orange roughy *Hoplostethus atlanticus*, walleye pollock *Theragra chalcogramma*, among others) that experienced overexploitation due to the severe underestimation of ages. Most validation studies of long-lived species to date have verified the periodicity and accuracy of growth marks for young individuals, but waiting for known-age fish to attain old ages is rarely utilized and may not always be feasible given the time required (Campana 2001).

Bomb-radiocarbon, radiochemical dating, release of known-age and marked fish, and mark-recapture techniques have been used or proposed to attain absolute age validation for long-lived fishes, yet these techniques often require substantial financial and time commitment from researchers to validate. The accuracy, commitment, and expense associated with these techniques will limit their use in many instances. For

example, bomb-radiocarbon is a technique that examines the amount of ^{14}C that was incorporated into the otolith of a fish after nuclear testing began in the 1950's. A small amount of ^{14}C indicates the pre-1958 era while elevated levels of ^{14}C indicate the era after nuclear testing. This approach is only applicable for those fishes where the presumed hatch dates span the 1960s and does not explicitly validate a certain age, only that it was hatched before or after nuclear testing began. This technique will eventually be unavailable for most fish species unless archived collections are used.

Mark-recapture techniques are well-suited for long-lived species and can be used to validate both the periodicity of growth increment deposition and the absolute age. When fish age is known at marking, either directly or inferred (i.e., young fish), absolute age validation can be performed when fish are recaptured. However, if fish age is unknown at marking, a calcium-binding chemical such as oxytetracycline, alizarin, or calcein can be applied at the time of tagging to create a permanent mark on the structure. Additional growth increments post-marking can be compared to the time at-large for recaptured fish to validate increment periodicity. These methods are the preferred methods for age validation outlined in Campana (2001) and the only perceived limitations are the rigors and cost associated with fish collections. This is particularly true with old fish as the probability of recapture decreases over time (Black et al. 2005). Though mark-recapture data is often difficult to collect, added benefits exist that warrant its use. For example, Paragamian and Beamesderfer (2003) used 23 years of white sturgeon (*Acipenser transmontanus*) mark-recapture data to estimate age and characterize growth patterns. In addition, various mark-recapture models can be used to determine population size, survival, and movement patterns (Kendall and Bjorkland 2001; Pine et

al. 2003). Therefore, the objective of our study was three-fold: to use mark-recapture data of known-age fish to attempt to validate both age and growth estimates generated from a commonly used aging structure from a long-lived sturgeon species, to demonstrate the applicability of using mark-recapture for determining growth patterns, and to predict age given a specified length.

Materials and Methods

We used a mark-recapture data set coupled with a previous age validation study for pallid sturgeon (*Scaphirhynchus albus*) to demonstrate the applicability of using these data to validate the accuracy of age estimates and to determine and predict age and growth characteristics. The pallid sturgeon is a long-lived, fluvial specialist endemic to the Mississippi and Missouri River basins (Bailey and Cross 1954; Dryer and Sandvol 1993). Many known-age and marked pallid sturgeon have been released as part of a Missouri River basin-wide propagation program. These known-age fish provided an opportunity to attempt to validate both age and growth estimates from a commonly-used aging structure, as this information will be critical for future recovery efforts.

The leading edge of the pectoral fin ray is the most commonly used age estimation structure for sturgeon of the genus *Scaphirhynchus*. This structure can be removed non-lethally (Koch et al. 2008) and has the highest reported precision compared to other structures (Jackson et al. 2007). However, the accuracy of age estimates obtained from pectoral fin rays (i.e., absolute age; Campana 2001) has not been successfully validated and several authors have suggested these data be used with caution

(Whiteman et al. 2004; Jackson et al. 2007; Kennedy et al. 2007; Killgore et al. 2007; Rugg, M.L., University of Nebraska-Lincoln, *unpublished data*).

Mark-recapture data for hatchery-reared pallid sturgeon from the 2001-2007 year classes were collected continuously by the Nebraska Game and Parks Commission in the Missouri River, Nebraska (river kilometers 811-1086). Mark-recapture events were included from pallid sturgeon that were at-large for a minimum of 30 days post-stocking or between subsequent recaptures. These data were compared to fin ray analysis from a previous study (i.e., same year classes) that attempted to validate juvenile pallid sturgeon age estimates (Koch et al. 2011). We assumed that mark-recapture data were the closest semblance to actual annual measurements of growth on wild fish and provided an opportunity to examine the bias and validity of using an aging structure (i.e., fin ray) to perform back-calculated growth estimates. Individual pallid sturgeon were distinguished with a unique tag or combination of tags (e.g., PIT tag, elastomer, scute removal) that identified the year class of the individual. All pallid sturgeon were measured to the nearest millimeter (fork length) at initial capture and subsequent recapture. Fin ray cross-sections and back-calculated measurements were provided by Koch et al. (2011).

The apparent bias in growth estimation between procedures was inferred from the comparison of observed growth increments from mark-recapture data to growth increments from length-at-age estimates generated from fin ray age data. Annual growth increments of mark-recapture individuals were calculated from the following equation:

(1) $G_i = \frac{(L_r - L_c)}{Y_i}$,

where G_i is the growth for fish i, L_c is the fork length at first capture, L_r is the fork length at re-capture, and Y_i is the number of years between capture events. To standardize the

data for various periods at large, we annualized the growth increment and expressed length as the median between capture events (Paragamian and Beamesderfer 2003).

Growth determinations using fin rays were estimated using traditional back-calculation techniques (Dahl-Lea method; DeVries and Frie 1996). Back-calculated length-at-age estimates provided by Koch et al. (2011) were generated with prior knowledge of age. Knowledge of age was needed to determine which mark was the first annulus due to disagreement between readers. Prior knowledge of age would theoretically reduce error in determining the number of annuli and should provide results that resemble true growth patterns, if annuli deposition in fin rays followed contemporary assumptions (e.g., proportional growth increments).

We also wanted to determine how back-calculated growth estimates would compare to other growth estimates without previous knowledge of age. Therefore, we solicited an independent age reader without knowledge of this study to age the fin ray sections analyzed by Koch et al. (2011) and make the appropriate measurements between presumptive annuli. The independent reader had prior experience aging shovelnose sturgeon and was instructed to disregard the hypothesized false inner annuli identified by Koch et al. (2011) so that results were directly comparable. Age estimates were compared to known ages with a two-sample *t*-test to determine accuracy.

Finally, we used an equal proportion approach to evaluate if other growth rates differed from a simple technique of dividing the fin ray into equal parts for each year the fish was alive. The assumption is that growth is equally proportionate throughout the entire life of the fish. This equal proportionate approach served as the null hypothesis that pallid sturgeon growth is linear. Linearized growth estimates for each method were

compared with an analysis of covariance (ANCOVA) using calculation method as a categorical variable and the median fork length as the covariate.

Von Bertalanffy curves were derived from mark-recapture data with a modification of the Fabens (1965) method. Growth increment data were fitted to the von Bertalanffy growth curve reformulated to account for observed growth between capture periods, so that,

(2) $\Delta L = (L_\infty - L_t)(1 - e^{-kT})$,

where ΔL is the increase in length between capture events $(L_{t+T} - L_t)$, t is time of tagging, T is the number of years between tagging and recapture, L_∞ is the von Bertalanffy length at infinity, and k is the von Bertalanffy growth rate coefficient. Parameters for the von Bertalanffy growth curve were estimated iteratively using a nonlinear regression approach. An estimate of the time at length zero (t_0) cannot be estimated with this method; therefore, we used the formula provided by Pauly (1979):

(3) $Log\ (-t_o) = -0.3922 - 0.2752\ Log\ L_\infty - 1.038\ Log\ k.$

Age (t) for pallid sturgeon of any given size (L_t) could then be estimated by using a reformulation of the von Bertalanffy equation (Kirkwood 1983):

(4) $t = t_o - log_e[(1 - L_t/L_\infty)/k]$.

Predicted ages were estimated with parameters derived from the mark-recapture data and were compared with corresponding average ages for pallid sturgeon of the same length that were determined using fin ray data.

Mean fork lengths (mm) for each of the seven year classes that were analyzed in this study (age-1-age-7) were calculated with each of the previously mentioned analytical procedures. Mean length-at-age was compared with a two-way ANOVA and pair-wise

comparisons of procedure-type for each age class were assessed with Tukey's studentized range test. All statistical tests used the statistical program R (ver. 3.0.0; R Development Core Team, 2013) and α level for all analyses was set at $P \leq 0.05$.

Results

There were 808 pallid sturgeon mark-recapture events that were at-large for 30 to 3,855 days (Figure 4.1). Annual growth was largest for small pallid sturgeon (< 300 mm) and declined to approximately 40 mm for pallid sturgeon between 300-750 mm fork length (FL) (Figure 4.2). As pallid sturgeon approached maturity (~ 800 mm; Keenlyne and Jenkins 1993), annual growth declined to approximately 20 mm (Figure 4.2). The estimate of average annual growth increment varied by the method of calculation ($P < 0.001$; Figure 4.3). Adjusted pair-wise comparisons (Bonferroni correction; $\alpha = 0.008$) indicated that back-calculated growth estimates from the fin ray aging structure with and without prior knowledge of age were different ($P = 0.002$). Back-calculated growth with knowledge of age resulted in a growth trajectory that declined much faster at larger sizes than growth that was observed from mark-recapture ($P = 0.003$). However, back-calculated growth without prior knowledge of age displayed a similar growth trajectory as the mark-recapture data ($P = 0.331$), presumably due to a large degree of age overestimation (Table 4.1). Both of these procedures (i.e., mark-recapture and back-calculations without knowing age) were not significantly different (i.e., the slopes were similar) from the null hypothesis of annual, equal proportionate growth (mark-recapture, $P = 0.01$; back-calculated w/o age, $P = 0.354$).

Accuracy of pallid sturgeon age estimates from the independent reader was lower than results reported by Koch et al. (2011). The reader's exact accuracy was 13% compared to the true ages of pallid sturgeon and increased to 43% within one year and 72% within two years of the true age. Similar to Koch et al. (2011), the reader generally overestimated the true ages due to the difficulty in discerning true annuli from presumed false annuli. Age estimates varied from 1 to 14 and the largest discrepancy in age was 8 years (Table 4.1).

Age for pallid sturgeon of any given size was estimated with parameters derived from mark-recapture data (Figure 4.4). The von Bertalanffy growth curve appeared similar to the actual length measurements observed from mark-recapture data. Mean length-at-age for all other calculation procedures was generally lower than the observed mark-recapture data (Figure 4.5). Pair-wise comparisons of mean length observed from captured fish of all age classes, but age-1, were similar to the predicted length-at-age from the von Bertalanffy equation.

Discussion

We used a combination of known-age pallid sturgeon (hatchery-reared) and mark-recapture data to corroborate previous attempts at absolute age validation and to determine growth rates for pallid sturgeon in the lower Missouri River. Our results suggest that mark-recapture data accurately portrays the growth trajectory of known-age individuals of a long-lived species and provides a means to estimate and validate basic rate functions related to growth. Our predictions of ages of individuals using the mark-

recapture approach compared to known age individuals was also successful through the years where we had such comparative capabilities.

Accuracy of pallid sturgeon age estimates from an independent reader was poor. These results are similar to Koch et al. (2011), providing further evidence to the inaccuracies of using fin rays for *Scaphirhynchus* sturgeon age estimation specifically, but likely applies to other long-lived species as well. Alternating concentric bands of translucent and opaque material are present in fin ray cross-sections; however, it appears that these marks do not necessarily relate to annular deposition or are too difficult to distinguish, leading to inaccurate counts. Both this study and Koch et al. (2011) found that age readers overestimated young pallid sturgeon (< age-7). However, annual growth becomes minimal for long-lived adults and age estimates from fin rays have been shown to underestimate true age in older individuals (Braaten, P., United States Geological Survey; *unpublished data*). A similar pattern has been shown in other fish species. Paragamian and Beamesderfer (2003) used mark-recapture data to determine that actual ages of white sturgeon *Acipenser transmontanus* were 1.5-2.0 times the ages estimated from fin rays. Lake sturgeon *A. fulvescens* age estimates from fin rays were also shown to underestimate the true age beyond age-14 (Bruch et al. 2009).

Growth estimates from mark-recapture data indicated that pallid sturgeon growth was fast during the first two years of life and then declined. Growth remained constant for the next few years until sexually maturity was presumably achieved. Estimating back-calculated growth with prior knowledge of age resulted in a different growth trajectory than growth observed from mark-recapture data. Back-calculated growth predicted much smaller sizes of young individuals followed by a steeper decline in

growth for older pallid sturgeon. Ironically, back-calculated growth without prior knowledge of age resulted in a similar growth trajectory as mark-recapture data. Overestimating age by several years forced the reader to make additional measurements to account for the extra, presumed annuli. Therefore, measurements between annuli were smaller and were more reflective of the growth that was observed from mark-recapture. These results further corroborate the inherent variability of using fin rays or other calcified structures that have not been validated for growth-based population dynamic metrics.

Using a reformulation of the von Bertalanffy growth equation, we inferred age of pallid sturgeon from observed growth data provided by mark-recapture analysis. Predicted fork length-at-age was similar to observations from mark-recapture data; however, our comparisons were limited to a maximum age of seven (Figure 4.5). The von Bertalanffy growth parameters derived from mark-recapture data provided a means to predict fork length-at-age for much larger individuals. These relations will require continued assessment to ensure that this trend holds throughout the life span of these fish, but look to be useful for examining age and growth of wild pallid sturgeon, where no known-age individuals exist.

Using our *Scaphirhynchus* sturgeon data as an example for evaluating age and growth in long-lived species highlights many shortcomings that Campana (2001) and others have mentioned repeatedly in the literature. Absolute age validation for *Scaphirhynchus* sturgeon fin rays has not been successfully implemented and previous growth assessments for *Scaphirhynchus* sturgeon have been conducted by examining mean back-calculated growth from age determination using fin rays (Hurley et al. 2004;

Whiteman et al. 2007; Koch et al. 2011; Rugg 2013). *Scaphirhynchus* sturgeon growth estimates generated from back-calculations are attractive because large volumes of age-specific growth data can be attained almost instantaneously from the time of capture. Further, age estimates from calcified structures (i.e., fin rays) are often used to determine age structure of the population and to determine mortality rates. This information is important for the management of *Scaphirhynchus* sturgeon populations throughout their range; therefore, it is not surprising that researchers continue to use fin rays for age and growth analysis even though several authors have urged caution to their accuracy (Hurley et al. 2004; Whiteman et al. 2004; Jackson et al. 2007; Kennedy et al. 2007; Killgore et al. 2007; Koch et al. 2011; Rugg 2013). Our results suggest that continued assessments of dynamic rate functions with the use of fin rays will likely provide inaccurate estimates and may lead to mis-management of the species as seen in several other long-lived fishes (Campana 2001).

The mark-recapture approach has been a standard approach to measuring growth (Quist et al. 2012), but has not been implemented often for long-lived species due to the perceived or realized difficulty in recapturing individual fish. Although mark-recapture techniques may require extensive sampling (and cost) to provide sufficient recaptures, these data may be useful in predicting ages of long-lived fishes that can be used to better understand age structure. Furthermore, additional analyses such as estimating population size, examining movement, determining emigration and immigration rates, and quantifying survival are often utilized with mark-recaptured data (Kendall et al. 1997; Cooch and White 2010; Steffensen et al. 2012). The wide breadth of information available from mark-recapture analyses should persuade researchers working with long-

lived species to implement a tagging program, particularly those working on long-term monitoring.

Our study provides an alternative approach to determining growth and estimating age of a long-lived species without the use of a calcified structure that may be subject to inaccuracies. Certainly, additional assessment of using the mark-capture approach to measure age and growth are needed, but this approach looks to have promise compared to other, less accurate or precise techniques. Using calcified structures may provide reliable results for some long-lived species if they can be validated; however, we recommend researchers understand the potential bias associated with these structures in long-lived species before adhering to conventional methods that have previously been conducted or are easier to calculate. In instances where age determination for all ages of interest cannot be verified, mark-recapture appears to be a viable solution for examining growth and has shown promise as a tool for estimating ages in long-lived species that have calcified structures too difficult to accurately and precisely read.

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Table 4.1. Comparisons of age estimates from an independent reader to the true ages of juvenile pallid sturgeon collected from the channelized Missouri River. Presented are the number of samples per age group, the mean age determination from the reader, and the range of age estimates from the reader for each of the age groups.

True Age	N	Mean age from reader	Range of ages from reader	Test statistic
1	3	2.7	2-3	$t = 8.00$, df = 2, $p = 0.015$
2	6	3.8	2-6	$t = 5.45$, df = 5, $p = 0.003$
3	10	5.1	3-7	$t = 10.00$, df = 9, $p < 0.001$
4	4	3.3	1-6	$t = 3.15$, df = 3, $p = 0.051$
5	9	6.8	3-11	$t = 9.26$, df = 8, $p < 0.001$
6	12	7.3	4-14	$t = 9.18$, df = 11, $p < 0.001$
7	2	4.5	4-5	$t = 9.00$, df = 1, $p = 0.070$

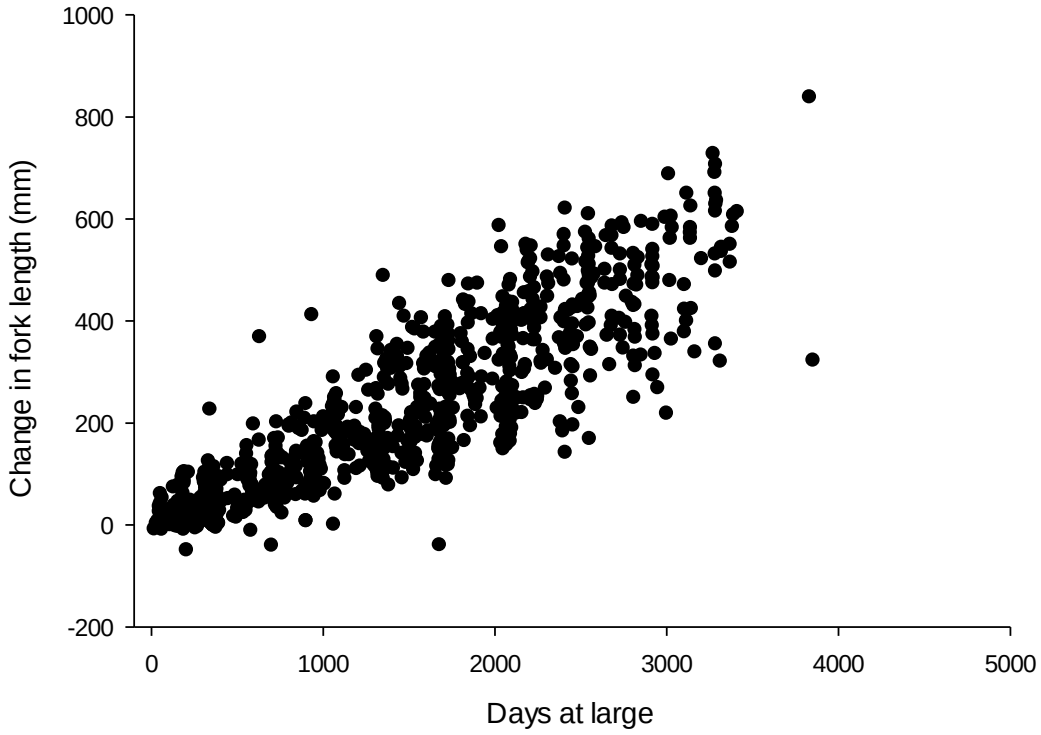

Figure 4.1. Change in fork length (mm) versus days-at-large of pallid sturgeon captured in the Missouri River (river kilometers 811-1086).

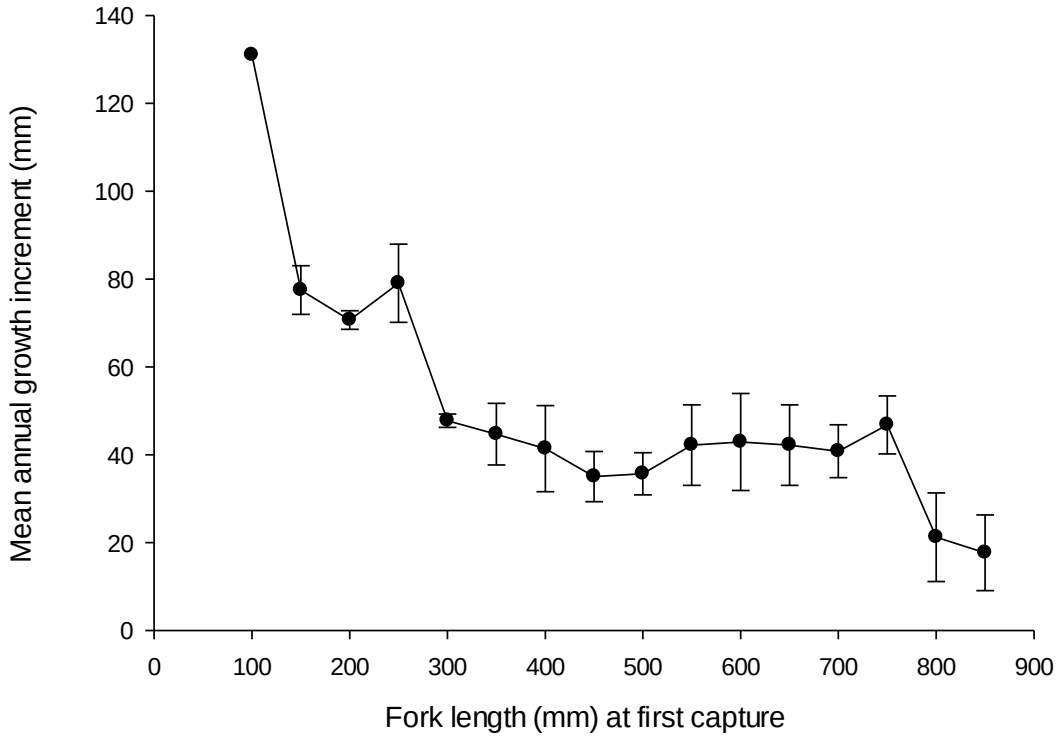

Figure 4.2. Mean (+/- SE) annual increment of growth for pallid sturgeon throughout the Missouri River (river kilometers 811-1086) derived from mark-recapture data. Fork length at first capture relates to the initial length at tagging and the subsequent growth that has occurred thereafter.

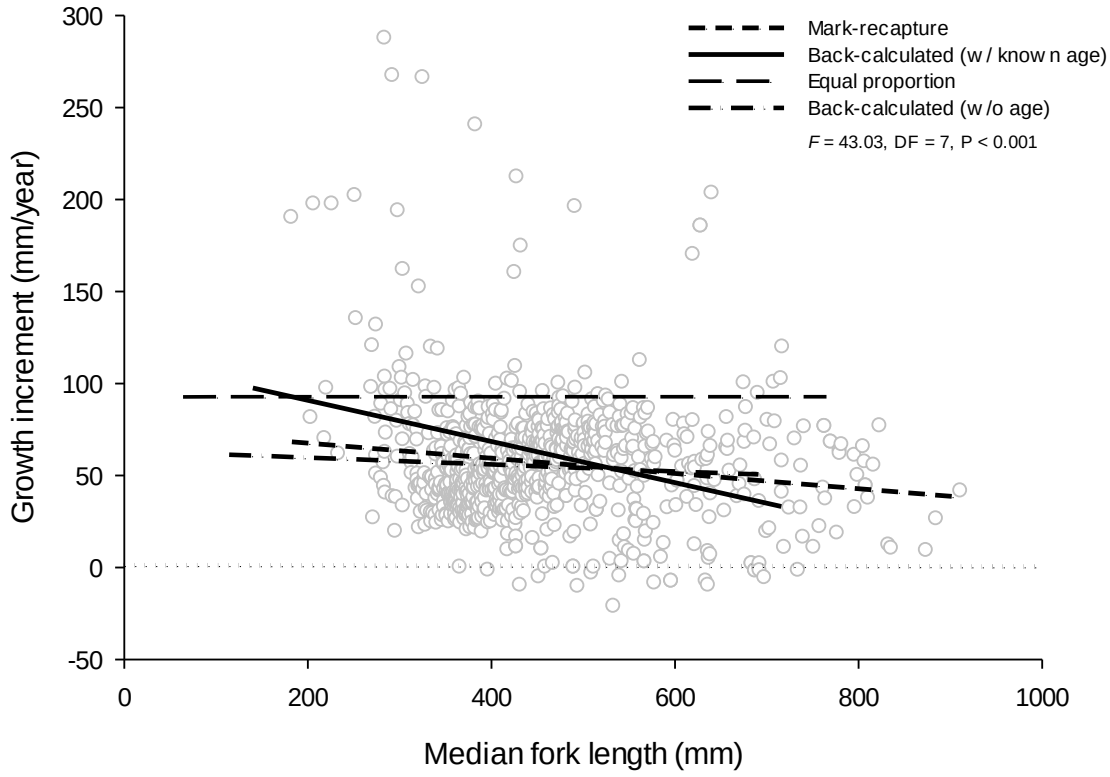

Figure 4.3. Average annual growth increment for the median fork length of pallid sturgeon computed with four alternative methods. Average annual growth was calculated from mark-recapture data (small dash), back-calculation procedures both with (solid line) and without (dash-dot line) prior knowledge of age, and assigning equal proportion of growth (large dash) throughout the fish's life span.

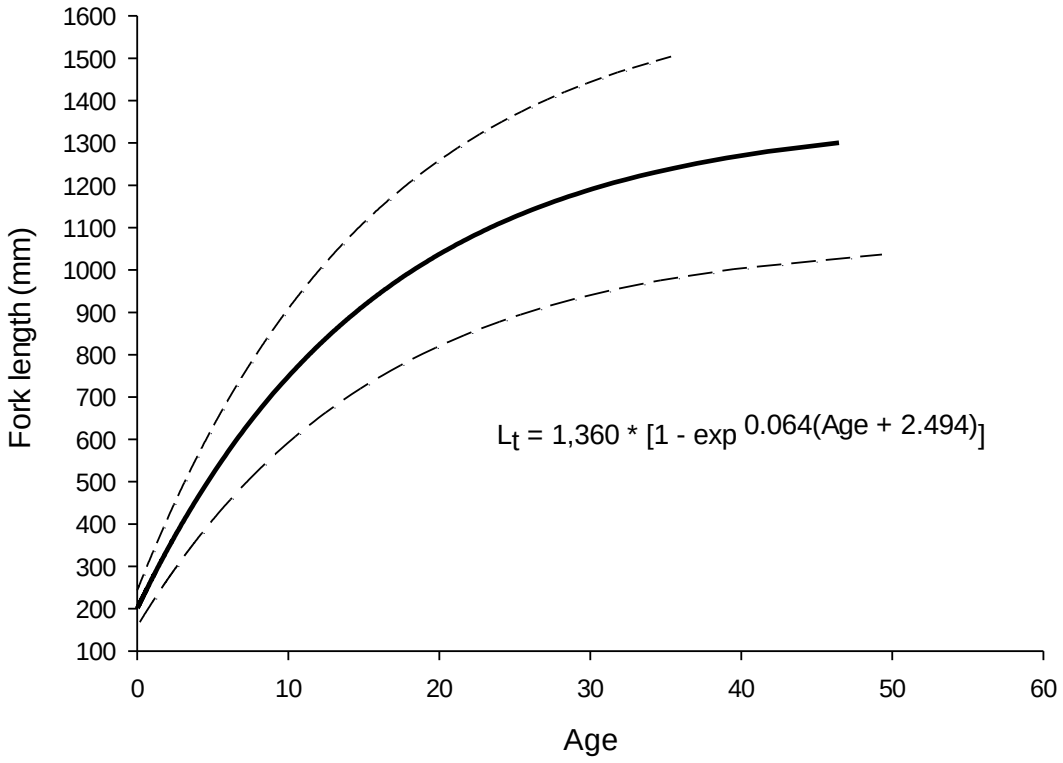

Figure 4.4. Length-at-age relations for pallid sturgeon derived from mark-recapture data. Growth increment data were fitted to a von Bertalanffy growth curve reformulated in terms of the increment of growth and the period of time between captures. Age for fish of any given size (Lt) was estimated with parameters derived from mark-recapture data.

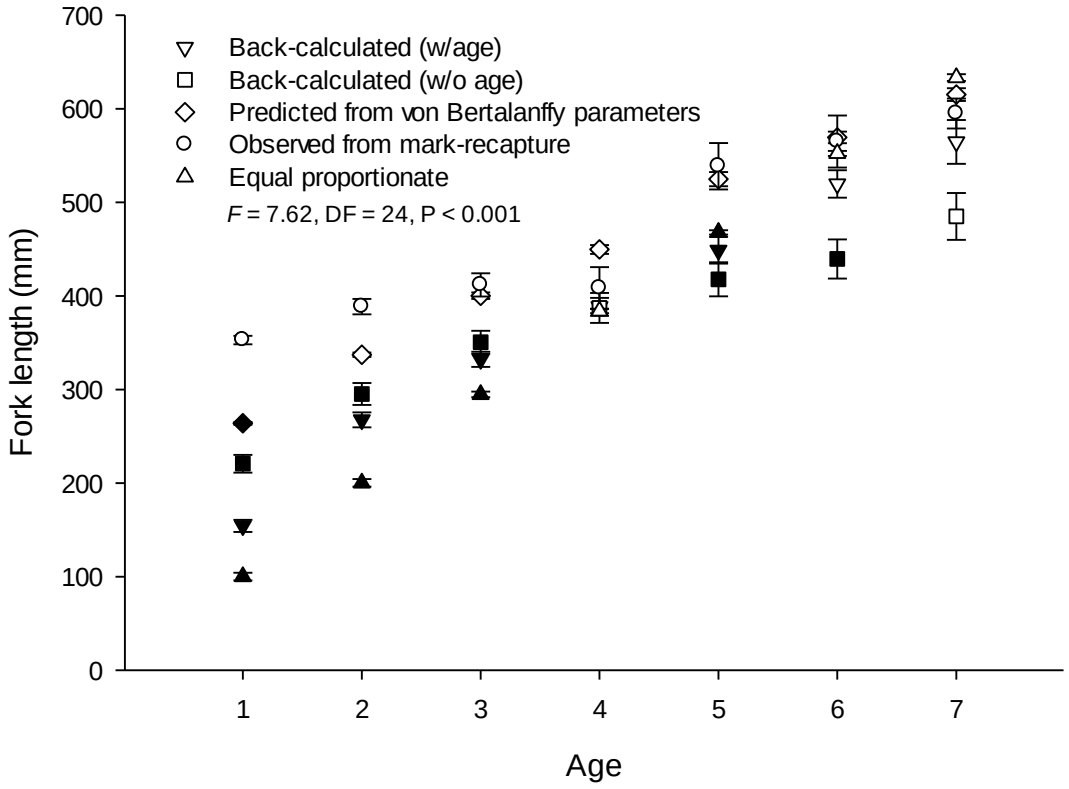

Figure 4.5. Mean (+/- SE) length-at-age (mm) computed from mark-recapture data, back-calculation procedures both with and without prior knowledge of age, and assigning equal proportions of growth throughout the entire fish's life span compared to actual observations of length from recaptured pallid sturgeon. Symbols with solid fill indicate a significant difference between the various methods of growth estimation compared to the actual observations of length observed from recaptures.

CHAPTER 5: SIMULATED VARIABILITY IN FIN RAY AGE ASSIGNMENTS AFFECTS POPULATION DYNAMIC RATE FUNCTIONS AND ESTIMATES OF LONG-TERM SUSTAINABILITY OF SHOVELNOSE STURGEON

This chapter is formatted for submission to Fisheries Research

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Abstract

Mortality, growth, and recruitment are the primary population dynamic parameters that regulate fish populations. Age data obtained from calcified structures can provide direct and indirect information needed for calculations of each of these parameters; therefore, knowledge of the fish population age structure is often coveted information for fish managers. Unfortunately, potential sources of error exist in the form of subjectivity in interpretation, consistent deposition of growth increments, and in the processing of aging structures when accuracy and precision have not been validated. Shovelnose sturgeon *Scaphirhynchus platorynchus* is a long-lived species that lacks a validated aging structure and reported precision between readers has been poor. Therefore, we conducted a sensitivity analysis to assess how variability in age assignments would affect calculations of growth, total annual mortality, and ultimately, affect population demographic models used for recovery or sustainability of shovelnose sturgeon in the Platte River, Nebraska. Simulated variation in age assignments (± 3 years) resulted in variable growth curves,

largely due to the influence aging error had on sub-adult fish (< age-6). Total annual mortality also varied by as much as 21% across the age precision simulations. These results were incorporated into a population viability model and sustainability was greatest when mortality rates were less than 20% and maximum age was greater than 15. Aging accuracy has not been validated and precision errors are common for shovelnose sturgeon and likely many other species that have had little or no age validation. The consequences of aging error should be considered when attempting to model population dynamics. Alternative methods for calculating population dynamic parameters should be assessed and conservative approaches should be used until accurate information is available.

1. Introduction

Mortality, growth, and recruitment are the primary population dynamic parameters that regulate fish populations because these parameters work synchronously to influence fish abundance and biomass. Age data can provide direct and indirect information needed for estimating each of the population dynamic parameters; therefore, knowledge of the fish population age structure is often coveted information (Quist et al., 2012). Age information is frequently obtained indirectly by inferring ages from growth increments observed on calcified structures. Unfortunately, potential sources of error exist in the form of subjectivity in interpretation, consistent deposition of growth increments, and in the analysis of aging structures when aging techniques have not been validated (Campana, 2001). Age validation for the respective calcified structure is therefore a prerequisite so that aging accuracy and precision can be quantified. Absolute age validation is difficult to assess because known-age fish are rare (Beamish and

McFarlane, 1983; Campana, 2001). In the absence of known-age fish, most researchers attempt to verify increment periodicity through various methods (i.e. chemical marking, mark-recapture, marginal increment analysis). If increment periodicity occurs in a consistent manor, those marks are inferred to be an accurate representation of the time scale observed and age can be determined (Campana, 2001). Verification of increment periodicity must occur across the entire age range of interest as growth patterns typically change throughout a species' life.

Age assignments for long-lived species are difficult because spacing of growth marks on calcified structures is minimal due to slow growth observed post maturity. Without absolute age validation for all ages, age estimates may be grossly underestimated (Campana, 2001). For example, walleye pollock *Theragra chalcogramma* aged with scales were thought to be a short-lived fish that can support high mortality rates from commercial harvest (> 40%; Beamish and McFarlane, 2000). After alternative structures were studied, an age validation study revealed that otolith cross sections frequently produced ages that were considerably older than from any other method and that a few strong year classes were responsible for the majority of the harvestable catch. Without these discoveries, the allowable harvest of walleye pollock may have been overestimated, leading to a potential collapse in the fishery (Beamish and McFarlane, 2000).

Sturgeons (Acipenseridae) represent an extant group of fishes that are long-lived and late-maturing and have received considerable attention in recent years due to range-wide declines linked to anthropogenic effects such as over-harvest, dam construction, and loss of habitat (Boreman, 1997). Nearly all European and Asian sturgeon species have experienced population declines and have subsequently been classified as either

threatened or endangered. North American sturgeons have experienced a similar plight in that all eight native sturgeon species are listed as endangered, threatened, or of special concern (Williams et al., 1989; Jelks et al., 2008). Pallid sturgeon *Scaphirhynchus albus* and shovelnose sturgeon *S. platorynchus* are congeners that are found throughout the Mississippi and Missouri river basins. Pallid sturgeon are federally listed as endangered (listed in 1990; Dryer and Sandvol, 1993) due to range-wide declines linked to dam construction, commercial harvest, and river modification for navigation (Bailey and Cross, 1954; Birstein, 1993; Keenlyne, 1997; Mayden and Kuhajda, 1997). Shovelnose sturgeon are the most abundant and widespread of North American sturgeons; yet, commercial harvest and habitat degradation have reduced their distribution and abundance (Keenlyne, 1997; Koch and Quist, 2010). Shovelnose sturgeon are classified as extirpated or at risk of extirpation in 50% of the states within their native distribution and many states have indicated either a decline in abundance or an unknown status (Keenlyne, 1997; Koch et al., 2009). Shovelnose sturgeon have also been recently protected from commercial harvest through a similarity of appearance clause in the Endangered Species Act where their distribution overlaps with pallid sturgeon (U.S. Federal Register 75 FR 53598, September 1 2010). Knowledge of the population age structure has been an integral component for assessment of these long-lived species so that demographic models used to predict population viability and responses to management actions could be evaluated (Bajer and Wildhaber, 2007; Koch et al., 2009; Jager et al., 2010; Steffensen et al., 2013). Further, age-structured models have commonly been used for determining mortality rates, spawning potential ratio, and

recruitment dynamics, particularly for shovelnose sturgeon in areas where they are still commercially harvested (Kennedy et al., 2007; Koch et al., 2009).

Attempts at validating the accuracy for aging *Scaphirhynchus* sturgeon with fin rays have had little success. Whiteman et al. (2004) used marginal increment analysis to validate annulus formation in fin rays from shovelnose sturgeon captured in the lower Missouri River. Although there were no statistical differences in marginal increment throughout the year, the authors concluded that most shovelnose sturgeon completed annulus formation in July and August. Rugg (2013) similarly used marginal increment analysis in the Platte River, Nebraska and found that monthly marginal increment measurements from fin rays did not display a yearly sinusoidal curve that would be expected if translucent and opaque bands represented one year of somatic growth. Hurley et al. (2004) conducted an absolute age validation study for pallid sturgeon by examining fin rays from 16, age-6 pallid sturgeon that were reared and held in captivity until fin ray removal. Results indicated poor accuracy as most age estimates were off by two years from the true age. To combat the affect captivity may have had on annulus formation, Koch et al. (2011) conducted a similar study with hatchery-reared individuals that were released into the wild during the first year of growth. The authors collected 36 individuals from 6 different year classes (age-1-age-7) and accuracy of age estimates among readers varied from 28 to 42%.

The cumulative effect of errors when using incorrect age estimates to determine population dynamic parameters is unknown. For example, several authors have shown that age-structured stock assessments are particularly sensitive to the chosen value of natural mortality (Mertz and Myers, 1997; Clark, 1999; Paragamian and Beamesderfer,

2003). Recently, Phelps et al. (2013) compared three methods of estimating mortality due to concerns of inaccurate age assignments. Total annual mortality calculated with age-based analyses (i.e. Heincke's method and catch curve) were 17% and 29%; whereas, total annual mortality calculated with a mark-recapture model was 35% (Phelps et al., 2013). These large discrepancies in parameter estimates could have an unforeseen effect when evaluating population demographic models to understand topics like population viability, particularly as most parameter sensitivity assessments only account for 5%-10% variation (Bajer and Wildhaber, 2007; Steffensen et al., 2013). Therefore, our objective was to assess how variability in age assignments using fin rays would affect calculations of growth and total annual mortality, as well as understand the effect on population demographic models used for recovery or sustainability of *Scaphirhynchus* sturgeon.

2. Material and methods

2.1 Data collection

Shovelnose sturgeon were collected annually from 2009 to 2011 in the lower Platte River, Nebraska. A multi-sampling gear approach was used to catch a variety of sizes and presumed ages of shovelnose sturgeon. Trotlines and trammel nets (see Chapter 2 for specifications) were deployed in equal representation throughout a variety of available habitat types throughout the year (March 1 – November 30). All shovelnose sturgeon were measured to the nearest millimeter (fork length; FL) and weighed to the nearest gram. The leading edge of the left pectoral fin ray was removed from all captured shovelnose sturgeon during the spring (March 1 – May 31) and fall (September 1 – November 30) seasons. Growth increment deposition was thought to occur during the

summer period; therefore, fin rays were not collected during June-August per recommendations by Whiteman et al. (2004). Fin rays were prepared using methods outlined in Pegg et al. (1998) and Koch and Quist (2007), where the fin ray is embedded in an epoxy-resin solution and later cross-sectioned. Fin ray cross-sections were mounted on microscope slides and photographed using a high resolution digital camera. Digital images were viewed for manual aging.

Three readers independently aged fin rays in 2009. Discrepancies in age determination between readers were re-evaluated by all three readers to develop a consensus age estimate. Reader agreement for all three readers was low (3% exact agreement) and among reader comparisons (i.e. combinations of only two readers) increased agreement slightly (11% - 21%). The leading edge of the pectoral fin ray is the most commonly used aging structure for *Scaphirhynchus* species because this structure can be removed non-lethally and has the highest reported precision compared to other structures (Jackson et al., 2007). However, the accuracy of pectoral fin rays (i.e. absolute age; Campana, 2001) has not been successfully validated and several authors have reported use with caution (Whiteman et al., 2004; Jackson et al., 2007; Kennedy et al., 2007; Killgore et al., 2007). Precision of age estimates in our study was low and was similar to previous studies for both *Scaphirhynchus* species. For example, the exact agreement between readers aging shovelnose sturgeon fin rays has varied from a low of 13% to a high of 81% in the literature (Morrow et al., 1998; Whiteman et al., 2004; Jackson et al., 2007; Kennedy et al., 2007; Koch et al., 2008). Fewer studies exist for pallid sturgeon and exact reader agreement has varied from 21% to 36% (Hurley et al., 2004; Killgore et al., 2007; Koch et al., 2011). Generally, reader agreement for

Scaphirhynchus sturgeon only approaches an acceptable level (~ 90%) when age estimates are within three years between readers. The percent agreement in our study ranged from 73% - 83% when age assignments between readers were within three years. As a result, independent age assignments by multiple readers were not conducted in 2010 and 2011. Two readers collectively aged shovelnose sturgeon fin rays to attain a consensus age estimate.

2.2 Data Analysis

Mean length and estimated age of shovelnose sturgeon from fin rays were used to estimate growth and mortality during 2009-2011. Growth of shovelnose sturgeon was described by fitting von Bertalanffy growth curves to length-at-age data from all three sampling years. The von Bertalanffy growth function is calculated as:

$$L_t = L_\infty \left[1 - e^{-K(t-t_o)}\right],$$

where L_t is the length at time *t*, L_∞ is the theoretical maximum length, *K* is the growth coefficient, and t_o is a time coefficient estimating when length is zero. Total annual mortality ($A \pm 95\%$ CI) was estimated with a weighted catch curve for all shovelnose sturgeon that recruited to the gear (> age-8) with at least five representatives per age group (Ricker, 1975; Van Den Avyle, 1993).

A sensitivity analysis was conducted to determine how variable age estimates effected calculations of total annual mortality and von Bertalanffy growth curve parameters. Age estimates derived from 2009-2011 shovelnose sturgeon fin rays (greater than age-5) were subjected to a series of simulations that randomly changed age estimates from 0-3 years (i.e. discrete uniform distribution). These years were chosen because

previous studies were mostly in agreement within ± three years. Calcified structures have been shown to underestimate long-lived fishes (Beamish and McFarlane, 1983), but we found no evidence of consistent under- or over-aging between reader agreements. However, we did want to determine if these patterns might affect growth and mortality estimates differently. Therefore, three different simulations were run to examine how aging errors might affect growth and mortality estimates when shovelnose sturgeon are over-aged, under-aged, or contain no consistent pattern of errors. The first simulation randomized the age component of the length-at-age data by allowing the assigned age to remain the same or add one to three years (i.e. simulated over-estimation of ages). For example, an age-7 fish could be reclassified as being from age-7 to age-10, while keeping the original associated length. The second simulation randomized originally assigned ages to remain the same or subtract one to three years (i.e. under-estimation). The third simulation randomized originally assigned ages to stay the same or vary either positively or negatively for one to three years. Simulations for each scenario were conducted only once to emphasize the potential error under common aging practices currently used (i.e. effects of 0-3 years), because the mean of many iterations would likely result in a common aging error (e.g. 0 ± ~ 1.5 years). For each simulation scenario, a catch-curve mortality estimate was calculated and the slopes of the catch-curve regression lines were compared between estimates with an analysis of covariance (ANCOVA). Similarly, von Bertalanffy growth curves were fit to the newly constructed age and length data. Comparisons of growth and mortality to the original estimates were used to demonstrate how divergent estimates influence key population dynamic parameters.

An age-structured population viability analysis (PVA) model was used to demonstrate how variable estimates of total annual mortality would affect an assessment of shovelnose sturgeon sustainability in the lower Platte River. Specifically, mortality estimates generated from previous simulations were used to model the estimated change in shovelnose sturgeon population size through time. The PVA model was developed by Steffensen et al. (2013) for pallid sturgeon and input parameters were modified for this study. See Steffensen et al. (2013) for details on model development. Fixed input parameters that were included in the model were gender ratio, spawning interval, and fecundity using data provided in Rugg (2013; Table 5.1). An estimated beginning population size of 20,149 individuals each sampling year was used for all simulations. This estimate was based on concurrent work in the Platte River (Hammen, J.J., unpublished data). Maximum age and annual survival rates for all shovelnose sturgeon greater than age-1 varied based on the previously discussed simulations. Stochasticity was not incorporated into the model so that the observed differences could only be attributed to the variable input parameters.

3. Results

Age estimates were generated for 1,707 shovelnose sturgeon fin rays from 2009 to 2011. Mean age of shovelnose sturgeon varied from 7.62 to 8.61 and there was a wide range of body lengths associated with each particular age (Fig, 5.1). Shovelnose sturgeon growth was initially fast during the first few years of life. Growth approached an asymptote near age-6 for each sampling year, but differences in growth of young fish (<

age-6) were apparent (Fig. 5.2). Total annual mortality estimated from the catch curves was similar among years ($F_{5,13} = 0.82$; $P = 0.463$) and varied from 36% to 47%.

Aging error simulations resulted in variable estimates of von Bertalanffy growth (Table 5.2). Growth patterns rarely mimicked the growth curve calculated from actual observations. The over-estimation simulation provided results that were most similar to the actual observations, whereas, the under-estimation and random error simulations were more influential in changing the growth curve related to aging error on sub-adult fish (less than age-6) (Fig. 5.3). Specifically, assigning large fish with young ages caused the growth curve to flatten.

Simulated total annual mortality estimates were highly variable and ranged by nearly a two-fold difference in some instances (Table 5.2). Our aging variability simulations resulted in mortality estimates that ranged from 17%-51% across years. However, tests for equality of the catch-curve regression slopes provided little evidence of separation of mortality estimates among simulations ($P > 0.131$; Table 5.2). The lowest mortality rates for each year were calculated with the random error and over-estimation simulations. Under-estimating age assignments provided mortality estimates that were similar to the original estimate and were typically 10-20% higher than the random error and over-estimation simulations.

The age-structured PVA model indicated that shovelnose sturgeon in the lower Platte River are not sustainable, given the original input parameters calculated from fin rays. Population declines would exceed 90% within 10 years using the maximum age and mortality rates calculated in 2009-2011 (Fig. 5.4). The lower mortality rates calculated in 2011 (A = 17% and 19%) with the over-estimation and random error

simulations indicated that the population would be greater than or equal to the original population estimate within a 20 year time period. The lowest mortality rate (i.e. 17%) would sustain the original population size through 40 years (Fig. 5.4). All other simulations resulted in mortality estimates greater than 30% and population sustainability declined, particularly after a 20-year period (Fig. 5.4).

4. Discussion

Estimates of growth and mortality were highly variable when age assignments were subjected to randomized error. These variable estimates could have drastic repercussions when making management decisions. Although *Scaphirhynchus* sturgeon fin rays have been documented as being notoriously difficult to age, this aging structure has provided the most precision in age assignments and can be collected non-lethally (Jackson et al., 2007). Multiple studies have urged caution for use in determining population dynamics (Whiteman et al., 2004; and others), but several studies have subsequently been published likely because other aging structures are not feasible, other methods are not well understood, or perceived slight inaccuracies are not thought to affect results (Scarnecchia et al. 2006; Tripp et al., 2009; and others). We concede that inaccurate age assignments within two or three years of the actual age may have fewer consequences when calculating dynamic rate functions for a long-lived species. However, this assumption would likely only be accurate if discrepancies in age assignments occurred toward the later-part of life in very old species (e.g. sablefish *Anoplopoma fimbria*; Beamish and McFarlane, 2000). We found that reader agreement between *Scaphirhynchus* sturgeon fin rays for small, presumably young, fish also

displayed poor precision and likely affected our estimates using both observed data and data simulated to emulate lack of age validation.

Comparisons of mortality rates were not significantly different from each other. However, mortality values used for modeling exercises are typically finite numbers, regardless of the variance, chosen from previous work or other studies (e.g. Bajer and Wildhaber 2007). Using the simulated estimates of natural mortality in the PVA model revealed differences in the predicted future population size. Estimates of mortality less than 20% suggest a population that would remain similar to the current size through a 20 year timeframe. Older maximum ages also had a positive effect on population size. All model predictions using the measured age assignments resulted in negative population growth. Previous work suggests that shovelnose sturgeon in the Platte River are common and have not exhibited substantial declines since research began in the late 1990s (Peters and Parham, 2008; Hamel and Pegg, 2013). Assuming the current population is stable; estimates of total annual mortality are likely being overestimated as a result of underestimating the age distribution of adult shovelnose sturgeon. Previous research has indicated that age-structured models are particularly sensitive to the chosen value for natural mortality (Clark, 1999) and is likely the reason for the predicted poor sustainability of shovelnose sturgeon in the Platte River.

Long-lived species are particularly difficult to age due to annulus crowding near the margin of the aging structure. These aging errors result in underestimation of the population age structure and provide overly optimistic estimates of growth and mortality that can potentially lead to population collapse. For example, orange roughy *Hoplostethus atlanticus* harvest has been re-evaluated because longevity was assumed to

be 20-30 years (Campana, 2001), but subsequent studies have found that orange roughy are capable of living over 100 years. Orange roughy also display extremely slow growth and coupled with their longevity are characteristics not suitable for quick population recovery to elevated harvest mortality (Smith et al., 1995). Sturgeon species display similar life-history strategies and attempts to validate various aging structures have shown that there is a tendency to underestimate longevity. Fin rays underestimated the true age and longevity was older than previous documentation for both pallid sturgeon and lake sturgeon *Acipenser fulvescens* when bomb radiocarbon techniques were used to attempt age validation (Bruch et al., 2009; Braaten, unpublished data). Similarly, white sturgeon *A. transmontanus* age estimates from fin rays were 30-60% less than apparent ages estimated from mark-recapture data (Paragamian and Beamesderfer, 2003). These studies demonstrate the propensity to underestimate long-lived species and provide anecdotal evidence that shovelnose sturgeon may be older than current research suggests. Continued reliance on unreliable age data may have important ramifications for understanding the ecology of *Scaphirhynchus* sturgeons by providing overly optimistic estimates of population dynamic rate functions.

We have demonstrated the potential inaccuracies when estimating mortality rates from non-validated aging structures and the ramifications for using these estimates to evaluate population level parameters for long-lived fish. Age-determination errors are an impediment to understanding population dynamics using conventional age-based assessments. Consequences of aging error should be considered when attempting to model population dynamic processes because aging accuracy has not been validated and precision errors are common. Alternative methods for calculating population dynamic

parameters should be assessed and conservative estimates should be used to prevent errors in management decisions.

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Table 5.1. Input parameters used in the shovelnose sturgeon population viability analysis model for the lower Platte River, Nebraska.

Variable	Value	Reference
Gender Ratio	0.50 : 0.50	Rugg (2013)
Maximum Age		
Observed	Age 18	This study
Simulations	Age 14-21	
Spawning Interval	Females = 5	Rugg (2013)
	Males = 3	
Age-at-maturity	Females = 6	Rugg (2013)
	Males = 6	
Absolute fecundity	16,098	Rugg (2013)
Survival rates	Egg to age-1 = 0.0004	Pine et al. (2001)
Observed	> age-1 = 0.63-0.74	This study
Simulations	> age-1 = 0.59-0.81	
Population estimate	20,149	Hammen[a] (unpublished data)

[a]Concurrent research on the lower Platte River

Table 5.2. Comparisons of total annual mortality (A ± 95% CI) and estimated von Bertalanffy growth parameters from fin ray age assignments of shovelnose sturgeon in the lower Platte River, Nebraska during 2009-2011. Also included are the mortality, von Bertalanffy growth parameter estimates (L_∞, is the theoretical maximum length, and K is the growth coefficient), and maximum age generated from a sensitivity analysis that simulated random variability and consistent over- or under-age assignments (± 3 years).

Year	Simulation type	A*	$L\infty$	K	Max age
2009	Observed	0.47 (± 0.12)	609	0.35	14
	Random error	0.34 (± 0.08)	611	0.14	17
	Over-estimated	0.34 (± 0.12)	597	0.32	17
	Under-estimated	0.51 (± 0.14)	615	0.01	14
	*$F_{5,15}$ = 2.33; P = 0.131				
2010	Observed	0.41 (± 0.10)	633	0.30	18
	Random error	0.31 (± 0.11)	1079	0.02	20
	Over-estimated	0.32 (± 0.12)	679	0.16	18
	Under-estimated	0.43 (± 0.11)	694	0.10	18
	*$F_{5,15}$ = 1.67; P = 0.221				
2011	Observed	0.36 (± 0.24)	651	0.19	14
	Random error	0.19 (± 0.10)	609	0.20	16
	Over-estimated	0.17 (± 0.19)	647	0.14	17
	Under-estimated	0.38 (± 0.25)	661	0.14	13
	*$F_{5,11}$ = 0.91; P = 0.435				

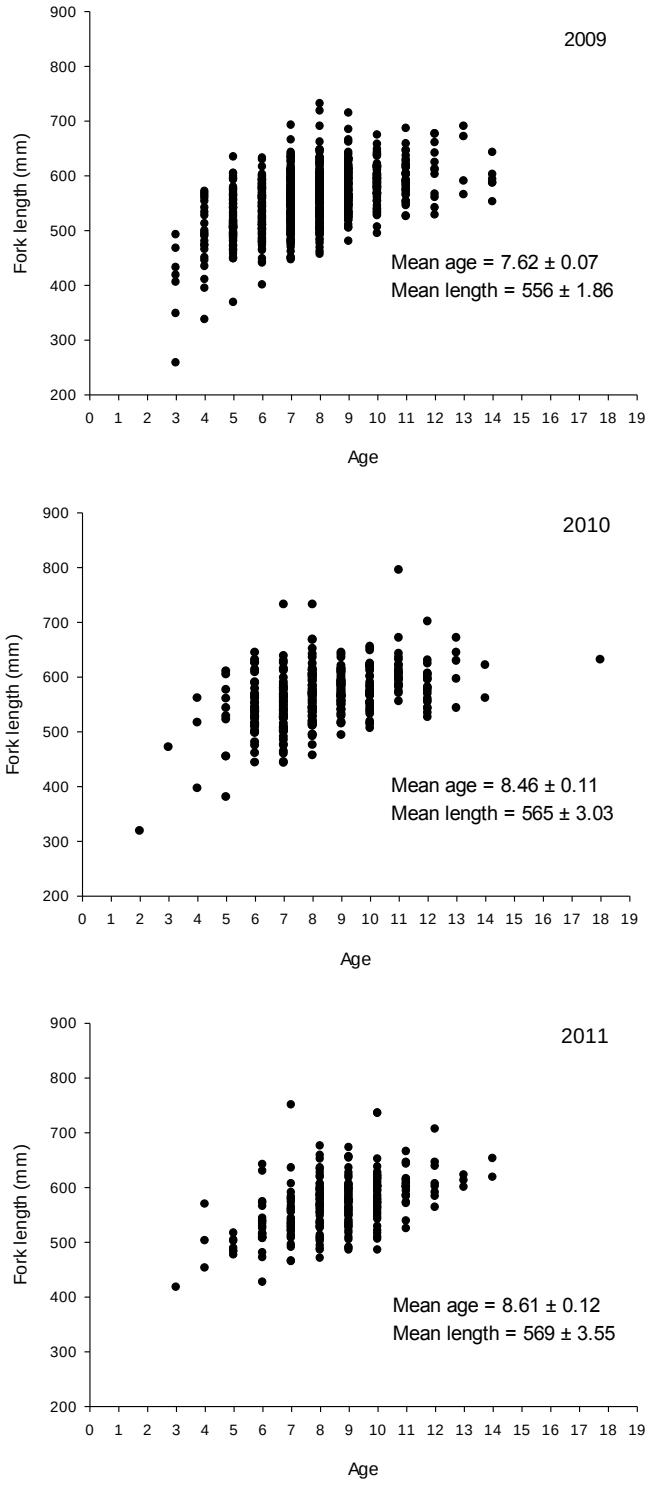

Figure 5.1. Fork length-at-age of shovelnose sturgeon collected during 2009-2011.

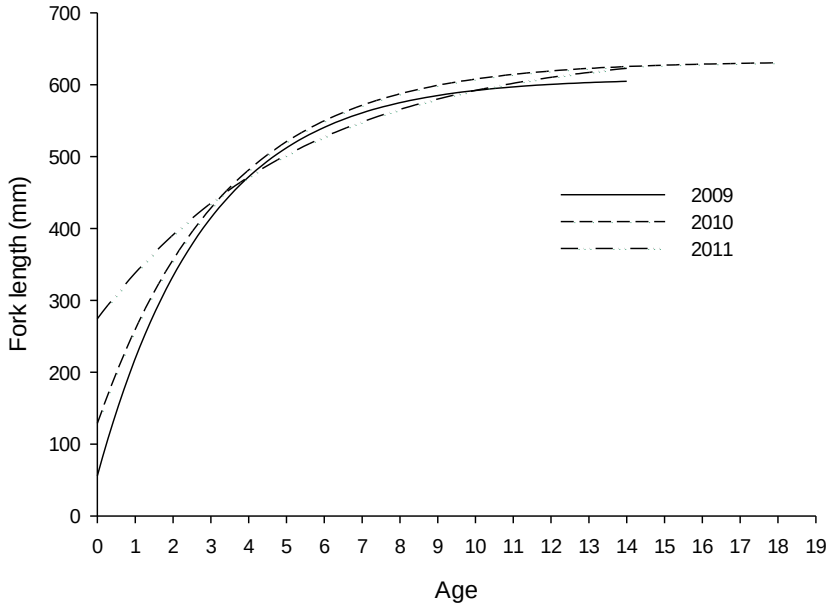

Figure 5.2. Growth curves for shovelnose sturgeon length-at-age data estimated from pectoral fin rays. Each line is the fitted von Bertalanffy growth function from 2009-2011.

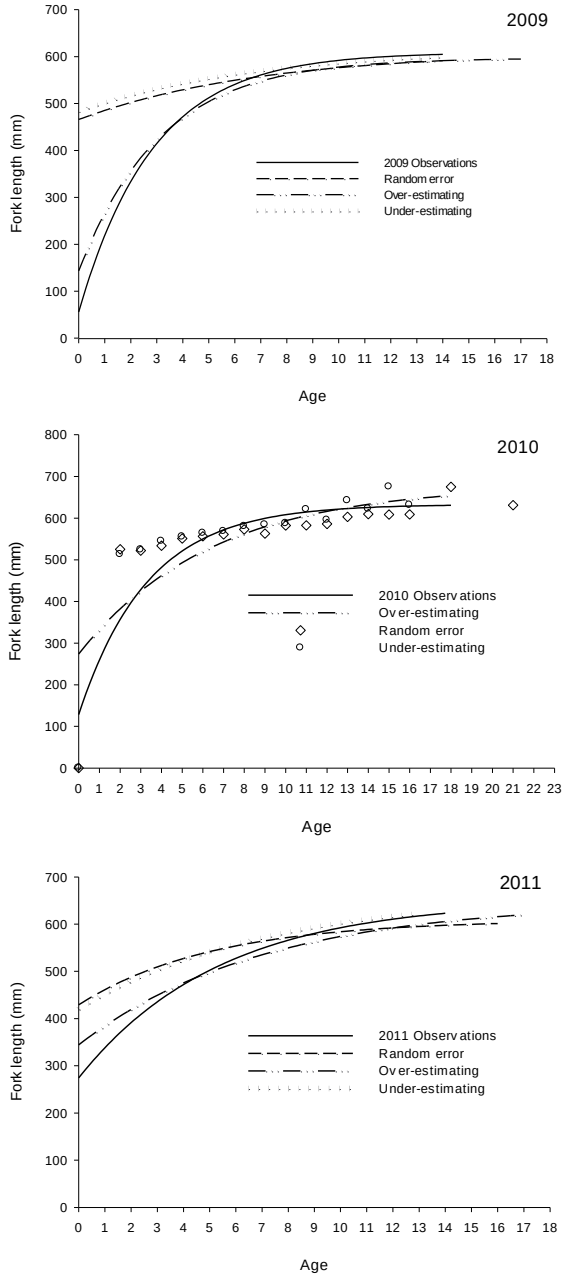

Figure 5.3. Fitted von Bertalanffy growth curve for the measured length-at-age data from 2009-2011 compared to von Bertalanffy growth curves where parameter estimates were generated from a sensitivity analysis that simulated random variability and consistent over- or under-age assignments (± 3 years). No line indicates lack of a relation ($P > 0.05$).

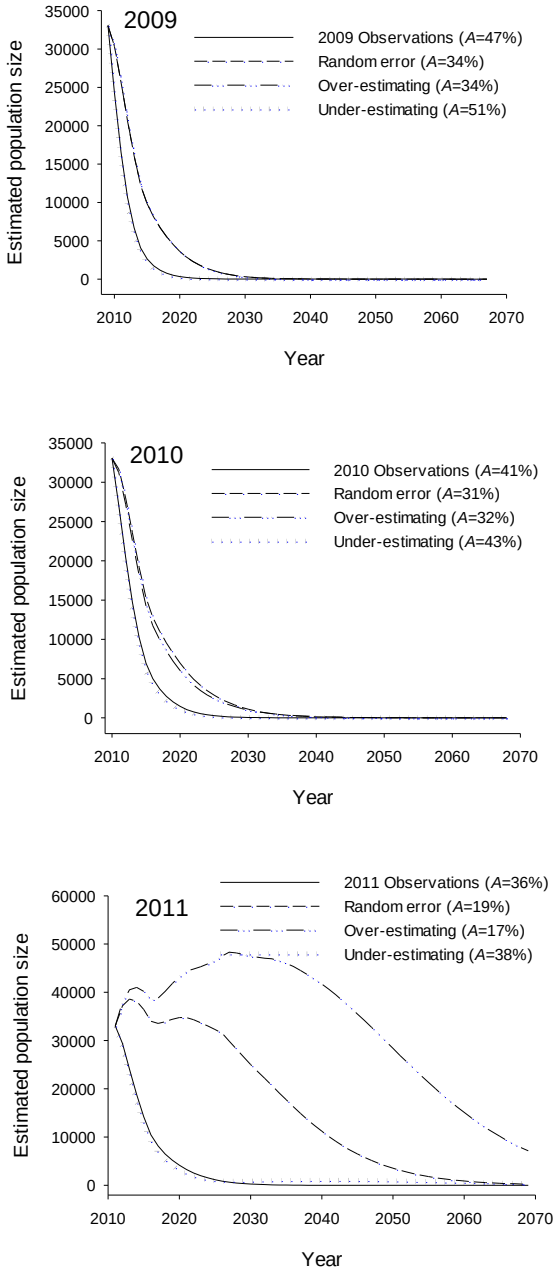

Figure 5.4. Predicted population size for all shovelnose sturgeon under varying levels of total annual mortality and maximum age. Mortality and maximum age were determined from a sensitivity analysis that simulated random variability and consistent over- or under-age assignments (± 3 years) from fin rays collected during 2009-2011.

CHAPTER 6: RANGE-WIDE AGE AND GROWTH CHARACTERISTICS OF SHOVELNOSE STURGEON FROM MARK-RECAPTURE DATA: IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

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Abstract

Shovelnose sturgeon (*Scaphirhynchus platorynchus*) are the most abundant and widespread of the North American sturgeons and inhabit large river systems throughout the Mississippi and Missouri river drainages; yet, commercial harvest and habitat degradation have reduced their distribution and abundance. We used mark-recapture data from shovelnose sturgeon to describe range-wide growth characteristics and developed a predictive model to estimate ages. Data were solicited throughout much of the current distribution of shovelnose sturgeon, specifically from the main-stem Missouri and Mississippi rivers and their tributaries. Shovelnose sturgeon exhibited variable growth among locations (i.e., populations). Adult fish from all populations exhibited almost no growth after they reached a particular size, presumably the size at sexual maturity.

Shovelnose sturgeon from the Mississippi River basin attained greater maximum sizes and ages compared to the Missouri River basin. However, two populations from the Mississippi River that received high exploitation from commercial harvest had truncated age distributions with smaller asymptotic lengths. Missouri River populations were characteristic of exploited populations (i.e., smaller fish and reduced longevity) presumably a result of anthropogenic effects. Wide discrepancies in maximum age and size suggest shovelnose sturgeon are capable of displaying phenotypic plasticity in response to exploitation or environmental influences. However, additional stressors (e.g., commercial harvest on the Missouri River) may have significant effects on population sustainability because plastic responses to increase reproductive output (e.g., further reductions in age or size at maturity) are likely not physiologically achievable. Determining metapopulation dynamics is a priority because it is unknown how population connectivity may influence dynamic rate functions and persistence of large-river fishes. Identifying potential source-sink connections in terms of population dynamics may provide a template for direction of future restoration and recovery efforts.

Introduction

Sturgeons (Acipenseridae) have experienced world-wide declines as a result of anthropogenic effects such as over-harvest, habitat degradation, altered flow regimes, and pollution (Birnstein, 1993). Sturgeons are migratory, long-lived, late-maturing fishes that do not spawn annually (Steffensen et al. 2013); a unique combination of traits that make them highly susceptible to human activities (Birnstein 1993; Birnstein et al. 1997; Pikitch 2005). Nearly all European and Asian sturgeons are considered either threatened or

endangered, and several species will likely soon become extinct (e.g., *Acipenser dabryanus*, *Psephurus gladius*; Birnstein 1993). North American sturgeons have experienced a similar plight in that all eight native sturgeon species are listed as endangered, threatened, or of special concern (Williams et al. 1989; Jelks et al. 2008).

Three North American sturgeon species are classified as river sturgeons (genus *Scaphirhynchus*), including shovelnose sturgeon (*S. platorynchus*), pallid sturgeon (*S. albus*), and Alabama sturgeon (*S. suttkusi*). Pallid sturgeon (listed in 1990; Dryer and Sandvol 1993) and Alabama sturgeon (listed in 2000; U.S. Federal Register 50 CFR 26445, May 5, 2000) are federally listed as endangered due to range-wide declines linked to dam construction, commercial harvest, and river modification (Birnstein 1993; Keenlyne 1997; Mayden and Kuhajda 1997). Shovelnose sturgeon are the most abundant and widespread of North American sturgeons and inhabit the large river systems throughout the Mississippi and Missouri River drainages (Keenlyne 1997); yet, commercial harvest and habitat degradation have reduced their distribution and abundance (Keenlyne 1997; Koch and Quist 2010). Shovelnose sturgeon are classified as extirpated or at risk of extirpation in 50% of the states within their native distribution, and many states have reported either a decline in abundance or an unknown status (Keenlyne 1997; Koch et al. 2009).

Shovelnose sturgeon have been harvested commercially throughout much of their range. Harvest reached a historic maximum in 2001 throughout the middle Mississippi River, likely due to increased commercial fishing pressure in response to the collapsed sturgeon fishery in the Caspian Sea (Birnstein 1993; Pikitch et al. 2005; Colombo et al. 2007; Tripp et al. 2009a). Shovelnose sturgeon harvest in the upper Mississippi River

exhibited similar patterns, as harvest in Iowa and Wisconsin more than doubled from 1997 to 2003 (Koch et al. 2009). In areas where shovelnose and pallid sturgeon are sympatric, incidental take of pallid sturgeon by commercial fishers has been documented due to their similarity in appearance (Bettoli et al. 2009). The U.S. Fish and Wildlife Service since listed shovelnose sturgeon as threatened under the similarity of appearance provision of the Endangered Species Act in 2010 (U.S. Federal Register 75 FR 53598, September 1, 2010) to further protect pallid sturgeon from commercial harvest. The area covered by this provision is limited to where the two species coexist (e.g., the middle Mississippi River). There is growing concern that increased harvest to meet international caviar demands will shift to shovelnose sturgeon populations that are not sympatric with pallid sturgeon without a solid grasp of what harvest could be sustainable.

Shovelnose sturgeon are migratory and often move between jurisdictional management areas (Bramblett and White 2001; DeLonay et al. 2007; Phelps et al. 2012). DeLonay et al. (2007) used telemetry to track movements of shovelnose sturgeon in the Missouri River during the spawning season and found that they moved an average of 216 km (both upstream and downstream movements). Migratory fishes are often susceptible to variable jurisdictional regulations such as harvest restrictions, seasonal fishing constraints, or length limits, and interjurisdictional management plans for large river species will likely play a role in future conservation and recovery (Pracheil et al. 2012). Coordinated regulations would ensure consistent conservation and management by providing a platform for communication and collaboration to assess range-wide issues. In addition, anthropogenic disturbances such as dams that block migration, altered hydrological conditions, and excessive harvest may further limit reproduction, dispersal,

or resource attainment. It is therefore critical to understand population dynamics throughout a species' range and how these dynamics might be influenced by regulations and habitat conditions.

Shovelnose sturgeon age and growth patterns are variable throughout their life history and geographic range. Shovelnose sturgeon typically exhibit fast growth for several years after hatching, with mean length at age-1 of ≈200 mm and annual growth of 50-75 mm per year thereafter until maturity (Kennedy et al. 2007; Killgore et al. 2007; Koch et al. 2009). Slow to minimal growth after maturity is commonly observed even though there is a large discrepancy in maximum size and age throughout their range (Kennedy et al. 2007; Killgore et al. 2007). Various hypotheses have been proposed to explain variation in growth among populations and include anthropogenic influences such as cold-water releases from dams that can reduce growth, unsuitable habitat that limits growth, and harvest of large individuals from commercial fishers (Everett et al. 2003; Koch et al. 2009; Tripp et al. 2009b). However, growth rates and maximum length also vary according to latitude (Conover and Present 1990). It is clear that factors driving age and growth in shovelnose sturgeon are complex, although effective range-wide management of this species requires improved understanding of how these factors influence populations across their distribution.

Determining growth is commonly assessed throughout an individual fish's life by back-calculating body length from annuli on calcified structures (e.g., scales, otoliths, fin ray or spine sections, etc.). Back-calculation is widely used in age and growth studies and increases the amount of growth data available for all age groups, especially young ages that may not be effectively sampled (Francis 1990). Interpreting age and growth

from calcified structures assumes that annuli are formed at a constant frequency and the distance between annuli is proportional to a fish's somatic growth (Campana and Neilson 1985). However, the accuracy of age estimates obtained from such structures is rarely successfully validated (i.e., absolute age; Campana 2001), and several authors have reported use with caution especially with shovelnose sturgeon (Whiteman et al. 2004; Jackson et al. 2007; Kennedy et al. 2007; Killgore et al. 2007). Recent work by Hamel et al., (*in review*) concluded that the assumptions of consistent annuli deposition and proportionality of annuli spacing to fish somatic growth are violated for *Scaphirhynchus* sturgeon. Presumed fin ray "annuli" were not congruent with age assignments, and estimates of growth from back-calculated estimates were overestimated.

Scaphirhynchus sturgeon growth information in the literature to date has been determined through the use of calcified structures. Given the concerns with using calcified structures to age shovelnose sturgeon, there is a great need to accurately assess growth characteristics throughout the species range. Our objective was to determine juvenile and adult growth, maximum sizes, and age estimates for shovelnose sturgeon populations throughout their distribution using mark-recapture data. We expected identification of differences in population dynamic metrics to provide insight into population-level differences in age and growth, as well as input parameters necessary to monitor and predict population viability.

Materials and Methods

Mark-recapture data were acquired from researchers throughout much of the current distribution of shovelnose sturgeon, specifically from the main-stem Missouri and Mississippi rivers and their tributaries (Figure 6.1). Mark-recapture data were obtained from six populations in the Missouri River, four populations in the Mississippi River, and five additional tributaries from within either basin (Table 6.1). We defined a population for this analysis as the specific management area where data were obtained. Some populations were relatively isolated (e.g., the Missouri River between reservoirs), whereas others were considered distinct due to hydrologic differences (e.g., tributary inputs), passable dams, or geographic location. Mark-recapture events were included from shovelnose sturgeon that were at-large for a minimum of 30 days between subsequent recaptures and all capture events for a given fish were confined to the defined population.

Growth of shovelnose sturgeon was assessed as the increase in somatic growth (i.e., fork length) between capture events for each individual within a population. Annual growth increments of tagged individuals were calculated using the following equation:

(1) $G_i = \frac{(L_r - L_c)}{Y}$,

where G_i is growth for fish i, L_c is fork length at first capture, L_r is fork length at re-capture, and Y is the number of years between capture events. Annual increment of growth was plotted by the initial length at first tagging to determine the size (i.e., fork length) at which growth begins to asymptote for each population. Only one growth measurement was recorded for fish that were recaptured multiple times and the longest period of time between captures was chosen to represent growth of that particular fish.

The observed growth increment of tagged juvenile shovelnose sturgeon was plotted relative to the years at large to quantify differences in growth among populations. Juvenile growth was examined because evidence suggests that shovelnose sturgeon exhibit minimal growth as adults; therefore, most somatic growth occurs during the juvenile time period (Killgore et al. 2007; Hamel, M.J. *unpublished data*). Juveniles were conservatively designated as less than 500 mm in the Missouri River basin (Rugg 2013) and less than 650 mm in the Mississippi River basin (Kennedy et al. 2006; Koch et al 2009), as most populations began to exhibit minimum growth after these sizes were attained. The slopes of the ensuing regressions of growth on size were compared among populations within each basin using an analysis of covariance (ANCOVA) to determine trends in growth patterns on a range-wide scale. We standardized the data for various periods at large to facilitate comparisons by pairing annual growth (G_i) to the midpoint in length between capture events ($[L_c + L_r]/2$) (Paragamian and Beamesderfer 2003). Statistical tests were conducted using SAS (ver. 9.2; Cary, North Carolina).

We developed von Bertalanffy curves from mark-recapture data of fish from all size ranges (i.e., juveniles and adults) using a modification of the Fabens (1965) method to estimate length-at-age. Growth increment data were fitted to the von Bertalanffy growth curve, reformulated to account for observed growth between capture periods, so that,

(2) $\Delta L = (L_\infty - L_c)(1 - e^{-kT})$,

where ΔL is the increase in length between capture events ($L_{c+T} - L_c$), L_c is time of tagging, T is the number of years between tagging and recapture, L_∞ is the von Bertalanffy length at infinity, and k is the von Bertalanffy growth rate coefficient.

Parameters (± 95% confidence intervals) for the von Bertalanffy growth curve were estimated iteratively using nonlinear regression (Gauss-Newton algorithm; Isely and Grabowski 2007). Age (*t*) for shovelnose sturgeon of any given size (L_t) could then be estimated by using a reformulation of the von Bertalanffy equation (Kirkwood 1983):

(3) $t = t_o - log_e[(1 - L_t/L_\infty)/k]$.

An estimate of the time at length zero (t_0) cannot be estimated with this method; therefore, we used the formula provided by Pauly (1979):

(4) $Log_e\,(-t_o) = -0.3922 - 0.2752\,Log_e\,L_\infty - 1.038\,Log_e\,k$.

Growth curves could then be generated with the newly calculated von Bertalanffy growth parameters, predicted ages, and fork length of shovelnose sturgeon.

Predicted length-at-age data (*t*) were used to characterize populations that may be exhibiting a truncation in size and age structure because these responses are likely a result of anthropogenic affects such as exploitation. Maximum ages were estimated as the oldest age predicted given the length corresponding to the von Bertalanffy growth parameter, L_∞. Furthermore, mean lengths at predicted ages were used to calculate the relative growth index (RGI) developed by Quist et al. (2003):

(5) $RGI = (L_t/L_s) * 100$,

where L_t is the mean of the previously described length at predicted age *t* and L_s is the predicted age-specific standard length. A mean length for each age was calculated by incorporating all lengths (in 1-mm increments) up to L_∞ into the age estimation formula provided by Kirkwood (1983). The age-specific standard length is estimated by calculating a von Bertalanffy growth model for all populations of shovelnose sturgeon

combined. Quist et al. (2003) stated that an RGI of 100 indicates that growth is average and an RGI above or below 100 is indicative of above or below average growth.

Results

Several populations of shovelnose sturgeon had many years between capture periods, whereas others had a much shorter duration between captures (Table 6.2). The overall mean time between captures of all individuals was 1.84 y and the greatest time was nearly 18 y, reiterating the capacity for shovelnose sturgeon to obtain old ages. Shovelnose sturgeon exhibited variable growth patterns between the main-stem Missouri and Mississippi rivers and their tributaries. Sturgeon from all populations exhibited nearly zero growth after they reached a particular size range, presumably the size at sexual maturity. The particular size when growth began to asymptote was variable. Growth of shovelnose sturgeon from the Missouri River basin began to asymptote at smaller sizes than fish from the Mississippi River basin. The asymptotic length for shovelnose sturgeon from the Missouri River was ≈ 500 mm (Figure 6.2). Tributaries of the Missouri River displayed a similar trend to the main-stem river (Figure 6.3). The asymptotic length for shovelnose sturgeon from the Mississippi River and its tributaries was more variable than the Missouri River and ranged from ≈ 500-650 mm (Figures 6.3 and 6.4).

Growth was faster for small (< 400 mm) individuals, but varied by population. Growth trajectories of juvenile shovelnose sturgeon < 500 mm from the Missouri River basin were typically steep (i.e., negative slope) (Figure 6.5). The upper Missouri River (rkm 2,525-2,851) displayed a positive growth trajectory for juveniles (i.e., growth

increment increased with size), but these results were likely skewed by small sample size (n = 8). The upper Missouri River population and the population below the lower-most dam (rkm 1,207-1,305) contained few individuals < 500 mm. Collectively, there was no statistical difference in slopes for growth increments by size of juvenile shovelnose sturgeon in the Missouri River basin ($F_{13,509}$ = 0.17, P = 0.9844). An inter-reservoir reach of the Missouri River (rkm 1,328-1,416) was not represented in this analysis as there were no fish < 500 mm in the sample.

Growth trajectories of juvenile shovelnose sturgeon from the Mississippi River basin were more variable than the Missouri River basin, resulting in differences in growth rates among shovelnose sturgeon populations ($F_{13,729}$ = 1.89, P = 0.093; Fig. 6.5). Portions of the upper (pools 20-26) and middle Mississippi River appeared similar to the Missouri River (i.e., fast growth at small sizes), although fish did reach a larger asymptotic size (Figure 6.5). Growth was slower for other regions of the Mississippi River basin and some populations (i.e., pools 8-12) did not asymptote until a length of ≈ 700 mm was obtained. Growth of juvenile shovelnose sturgeon from the Mississippi River basin tributaries exhibited slow growth for all sizes compared to Mississippi River juveniles, despite asymptoting at a larger size.

Age estimates for shovelnose sturgeon of any given size was estimated using mark-recapture data. Maximum age varied widely throughout populations of shovelnose sturgeon, particularly in the Mississippi River basin (Figures 6.6 and 6.7). Shovelnose sturgeon from the Wabash River and Atchafalaya River were not included in this analysis due to low (n = 31 and 15) sample sizes. The Wisconsin River population had a small estimated growth coefficient (K) where there was minimal growth between capture

periods for large fish (> 650 mm), leading to a particularly high maximum age estimate (Fig. 6.8). Pools 20-26 in the Mississippi River exhibited the largest discrepancy in asymptotic size and predicted ages in relation to other populations throughout the Mississippi River basin. Growth began to asymptote as small as 500 mm and the maximum ages were predicted between 12 and 13 y. Results from the middle Mississippi River (rkm 201 – rkm 0 [Ohio River confluence]) were similar (predicted age ≈ 18), and all other populations from the Mississippi River basin displayed a much larger asymptotic size (> 650 mm) and maximum age (Figure 6.6). Maximum age estimates in the Missouri River basin were typically lower, and growth began to asymptote at lower ages (Figure 6.8). Relative growth index values varied from 75-173 among all populations and ages (Table 6.3). Similar to growth trajectories of young shovelnose sturgeon, RGI values were typically greater in the Missouri River basin compared to the Mississippi River basin.

Discussion

Shovelnose sturgeon displayed phenotypic plasticity in growth among populations throughout their distribution. Maximum size of shovelnose sturgeon from the Missouri River basin was typically smaller and growth began to asymptote at smaller sizes compared to other populations. The one exception to this trend was the population of shovelnose sturgeon in the upper Missouri River in Montana that attained maximum sizes comparable to populations from the Mississippi River. Maximum size and length when growth began to asymptote was more variable from the Mississippi River basin. The upper Mississippi River basin was characterized by large fish that displayed continuous,

albeit slow, growth. Conversely, shovelnose sturgeon from the middle Mississippi River grew fast and began to asymptote at smaller sizes. Estimated ages were lower in populations of shovelnose sturgeon that displayed a smaller asymptotic length range. Similarly, high RGI values corresponded to populations that exhibited smaller asymptotic sizes and lower predicted ages.

Several hypotheses may explain discrepancies in maximum size and growth exhibited throughout the distribution of shovelnose sturgeon. First, growth rates and maximum size have been known to naturally vary according to latitude (Conover and Present 1990), and two competing hypotheses describe how latitudinal compensation in growth might evolve. One hypothesis is that genetic variation in growth rate results from adaptation to temperature. Growth rates for populations across various latitudes are typically maximized at the temperature most commonly experienced (Yamahira and Conover 2002). In other words, fishes from high-latitudes will have maximum growth rates at lower temperatures than fishes from low-latitudes. The second hypothesis (i.e., counter gradient variation) focuses on length of the growing season rather than local mean temperature. In this case, fishes living in high-latitudes are subject to a shorter growing season because the duration of colder water temperatures are extended (i.e., longer winter). These individuals compensate for the shorter duration by evolving a higher overall capacity for growth (i.e., greater growth rates). Maximum growth still occurs at the same temperatures as low-latitude individuals, but high-latitude fishes grow proportionately faster across all temperatures that permit growth (Conover 1990; Conover and Present 1990; Marcil et al. 2006). Shovelnose sturgeon within the Missouri and Mississippi rivers did have some of the largest maximum sizes occurring in populations

from the northern-most latitudes. However, shovelnose sturgeon from corresponding latitudes between the Missouri and Mississippi Rivers did not display similar size ranges. For example, fish collected in the upper Mississippi River (pools 8-10) were at a similar latitude as fish from the upper un-channelized region of the Missouri River (rkm 1207-1305), but maximum size is larger in the Mississippi River. Furthermore, shovelnose sturgeon from the Wabash River, which is located in the middle region of the latitudinal gradient among sites, had some of the largest fish of any population in our dataset. The influence of latitude on growth cannot be ruled out, but it seems there are likely other contributing factors that are responsible for observed differences. Factors such as food availability, habitat modification, and biotic interactions are likely the driving forces behind growth rates, particularly in systems that have been modified from their original states (Pegg and Pierce 2001).

Somatic growth is an indication of population health related to food resources and habitat quality (Pope et al. 2010). Fast growth suggests that fish density is not limited by food resources and habitat quality is sufficient. Slow growth can indicate insufficient habitat to support an adequate prey base or fish density that is too high relative to the available food source (Pope et al. 2010). Fish growth also influences age and size at sexual maturity. The amount of energy available from the environment after intra- and inter-specific competition ultimately determines how quickly an individual will achieve sexual maturity (Trippel 1995). In a heavily exploited population, intraspecific competition is reduced, allowing greater food intake per individual and thus faster growth. Early maturation can be achieved as a result, and is presumably an adaptation, that allows individuals to achieve maximum reproductive output in a lifetime, thus

permitting population size to increase over a shorter period (Stearns and Koella 1986; Trippel 1995; Hutchings and Reynolds 2004). Shovelnose sturgeon have been commercially harvested for a number of years, but recent market pressure has increased harvest (Colombo et al. 2007; Koch et al. 2009; Tripp et al. 2009a), particularly in the middle Mississippi River. Shovelnose sturgeon in the middle Mississippi River appear to have responded to the increase in exploitation as they exhibit smaller asymptotic sizes and younger predicted ages than populations from areas both upstream and downstream of this location. The recent commercial fishing closure where shovelnose sturgeon distributions overlap with those of pallid sturgeon may alleviate reductions in abundance and evaluating any population responses to this closure will advance further understanding of conservation needs for the species.

Commercial fishing harvest in the navigation pools is lower compared to estimates from the middle Mississippi river. For example, the Iowa Department of Natural Resources reported total harvest of shovelnose sturgeon from commercial harvesters fishing along the border waters of the state (i.e., pools 8-19) to be 1,492 kg in 2004 (Koch et al. 2009), whereas harvest along the border waters of Missouri approached 60,000 kg annually in the early 2000's (Colombo et al. 2007). With the commercial fishing closure due to the SOA act in the middle Mississippi River, commercial fishing pressure could be re-directed to the upper Mississippi River. Increased harvest could have severe impacts for population viability. Declines in asymptotic size and maximum age have already been observed and populations composed of small individuals and lower maximum ages may have reduced reproductive potential (Hutchings and Reynolds 2004) given that fecundity often increases with female size (Trippel 1998). Collectively,

these effects may reduce the potential for conservation or recovery and result in a recruitment overfishing scenario where the end result is a collapse of the fishery (Myers et al. 1994).

The Missouri River is largely exempt from commercial fishing harvest. The state of Missouri was the only state that allowed commercial shovelnose sturgeon harvest in the Missouri River prior to the SOA act. Exploitation was relatively low compared to the Mississippi River, and estimates in the late 1990's and early 2000's were approximately 500 kg/year (Quist et al. 2002). Despite low harvest, populations of shovelnose sturgeon from the Missouri River basin displayed growth characteristics of a heavily exploited fishery. Growth from nearly all Missouri River populations began to asymptote at a small size (i.e., 450-500 mm), and predicted ages were truncated to approximately 15-25 years. As harvest is minimal throughout most locations of the Missouri River, the observed compensatory growth responses are likely a function of responses to environmental conditions. The Missouri River has been highly altered with the construction of six main-stem dams in the upper river and channelization to allow for deep-draft barge traffic in the lower Missouri River (Hesse and Mestl 1993; Pegg et al. 2003). In the upper Missouri River basin, short reaches of relatively unaltered (i.e., unchannelized) river exist between reservoirs. However, hypolimnetic releases from these dams have altered the temperature regime, sediment dynamics, and affected the natural flow regime (Hesse 1987; Poff et al. 1997). The upper-most population of shovelnose sturgeon was from a 340-km reach of river below Fort Peck dam, Montana. This reach exhibited shovelnose sturgeon growth that was more characteristic of

populations from the upper Mississippi River; that is, growth was slower and fish attained larger sizes.

Channelization of the lower 1,207 km of the Missouri River has transformed a once natural, complex floodplain river to a relatively artificial, simple system (Pegg et al. 2003). Channel morphology has been changed from a natural "V-shaped" channel with frequent floodplain inundation to a "U-shaped" channel with relatively uniform depths and velocities (Hesse and Sheets 1993). This environment lacks historical fluvial characteristics (e.g., main-channel sandbars, natural chutes and backwaters, and refuge habitat) and may have increased natural mortality rates, ultimately functioning as a surrogate for high exploitation. This potential for habitat loss to act as a surrogate for high levels of exploitation (i.e., harvest) has not been fully evaluated for shovelnose sturgeon. Given the pervasive losses of large river habitats in the Mississippi and Missouri River basins, future research efforts to support conservation and management of shovelnose sturgeon and other large river fishes should focus on the interplay of direct and surrogate exploitation as a factor in population viability.

Adult shovelnose sturgeon exhibited a distinct pattern of nearly zero growth between recaptures. This pattern is unusual as fish growth is typically believed to be indeterminate (Weatherley and Gill 1987). Shovelnose sturgeon growth characteristics resemble higher vertebrates where maximum sizes are achieved and are not surpassed even during abnormally long lifetimes. However, studies have shown that fish growth may resume when there is a return to optimal conditions (Bertalanffy 1960; Weatherley and Gill 1987) and continued observations are needed to corroborate this assertion. We assumed that the length when growth begins to asymptote was related to the size at

reproductive maturity. This assumption was based on several studies examining the reproductive biology of shovelnose sturgeon that reported sexual maturity in the Missouri River and the lower Platte River at approximately 450 mm (Moos 1978; Rugg 2013); whereas fish from the upper and middle Mississippi River and the Wabash River were first mature at approximately 570-615 mm (Kennedy et al. 2006; Koch et al. 2009; Tripp et al. 2009b). The length at maturity of shovelnose sturgeon varied by populations and appeared to be influenced by abiotic or biotic factors. The asymptotic size may be a good indicator for system health because fish that asymptote in length at larger sizes attained older ages. The asymptotic size therefore and may be a benchmark to set future management objectives or conservation goals against.

Though distinct differences in age and growth were observed between some river reaches throughout the Missouri and Mississippi river basins, a number of the populations we examined reside in an open system where fish have the freedom to move among and within management areas. The spatial extent that shovelnose sturgeon complete all or portions of their life-history is not well understood. However, long distance migrations of shovelnose sturgeon are common (DeLonay et al. 2007), and previous research suggests that fish movement plays an important role in transporting different life stages across various landscape scales to occupy suitable habitats that are required to fulfill their life cycle (Schlosser and Angermeier 1995). The recaptured fish in our dataset were from the same management area in which they were originally captured and tagged. Several mark and subsequent recaptures from the Platte River, NE were within a 1-km reach of river after numerous years at large; however, some individuals did move several hundred kilometers between sightings. Exact movements

and behavior between captures is unknown, but there appears to be a certain degree of fidelity to suitable habitat patches in at least some instances. Having access to the suitable habitat sites through appropriate river connectivity would therefore seem to be crucial. Further research is needed to evaluate the importance and degree of movement between populations to better understand the metapopulation dynamics of shovelnose sturgeon (Leibold et al. 2004). Recent work by Phelps et al. (2012) used fin ray microchemistry to identify river of origin for age-0 *Scaphirhynchus* sturgeons in the Missouri and Mississippi rivers. Fin ray microchemistry appears to be a legitimate tool for determining natal origin, but may also be beneficial for determining movement patterns of adults and juveniles between river systems and within river segments.

Implications for Conservation and Recovery

Mark-recapture data from across the distribution of shovelnose sturgeon have provided insight into the current condition of various populations. Shovelnose sturgeon displayed phenotypic plasticity in maximum size and growth, likely as a result of anthropogenic influences such as commercial harvest and river modification. Shovelnose sturgeon possess life-history characteristics that have likely made them more resilient to reductions in abundance than other species of sturgeon such as a smaller size, younger age at maturity, and a shorter duration between spawning events (Keenlyne 1997; Morrow et al. 1998). Nevertheless, several populations of shovelnose sturgeon appear to be at risk of immediate or future declines. The lower portion of the impounded Mississippi River (pools 20-26) may be susceptible to declines due to the potential for increased commercial harvest on a population of fish that has already exhibited smaller

asymptotic and maximum sizes as well as a truncated predicted age distribution. Reaches of river below dams in the Missouri River appear to be influenced by modified flow regimes (i.e., thermal influence, reduced turbidity, stable flow) and may rely completely on movement from source populations for recolonization. The lower Missouri River basin (i.e., the 1,207 km of the channelized Missouri River and its tributaries) may be operating under a hybrid metapopulation dynamic model, where high dispersal among important habitats that are necessary for carrying out life-history stages has led to persistence over time (Falke and Fausch 2010). Small asymptotic and maximum sizes in relation to most areas of the Mississippi River basin indicate these populations may be subject to hastened declines in the presence of additional stressors (e.g., commercial harvest on the Missouri River, climate change) in the face of current pressures on the populations.

Many tributaries of the Missouri and Mississippi rivers contain populations of shovelnose sturgeon that were not included in this analysis. Tributary streams are important components to main-stem rivers, providing use for fish spawning and reproduction, nursery or refuge habitat, complexity of habitat types, and areas for foraging (Dames et al. 1989; Osborne and Wiley 1992; Rice et al. 2001; Pracheil et al. 2009; Neely et al. 2010). Although tributary streams play some functional role in the ecology of large rivers, the importance of tributary streams is not completely understood. For example, some of the more highly regarded concepts in river ecology have largely overlooked the potential influences tributaries might have on energy inputs, fish species richness, and their spatial location within the river network (Vannote et al. 1980; Junk et al.1989; Thorpe and Delong 1994). Furthermore, tributary streams are often relatively

unaltered compared to main-stem rivers and may provide a viable opportunity for conservation of large-river fishes (Pracheil et al. 2013). Restoring the main-stem Missouri and Mississippi rivers is unlikely, and even gaining social acceptance to support rehabilitation will be challenging (Jacobson and Galat 2006). Identifying tributaries and determining their relative importance and contributions (e.g., metapopulation dynamics) may be key for conservation of large river fishes such as sturgeon. Persistence of large-river fishes will likely depend on population connectivity at multiple scales, and identifying these connections will be key for developing a template for future restoration and recovery efforts.

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Table 6.1. Sources contributing data to this study and the locations from where data were collected.

Agency/Institution	Area of collection
Montana Fish, Wildlife, and Parks	Missouri River (rkm 2,523 - 2851)
U.S. Fish and Wildlife Service - Great Plains office (PSPAP*)	Missouri River (rkm 1,328 - 1,416)
South Dakota Game, Fish, and Parks (PSPAP)	Missouri River (rkm 1,207 - 1,305)
Nebraska Game and Parks Commission (PSPAP)	Missouri River (rkm 789 - 1,207)
Missouri Department of Conservation (PSPAP)	Missouri River (rkm 402 - 789)
U.S. Fish and Wildlife Service - Columbia Field Office (PSPAP)	Missouri River (rkm 0 - 402)
University of Nebraska	Platte River
Missouri Department of Conservation (PSPAP)	Kansas River
Wisconsin Department of Natural Resources (DNR)	Mississippi River (Pools 9 & 10)
Iowa DNR	Mississippi River (Pools 11 & 12)
Missouri Department of Conservation	Mississippi River (Pools 20-26)
Missouri Department of Conservation	Mississippi River (rkm 201 - OH River confluence)
Wisconsin DNR	Wisconsin River
Purdue University and Indiana DNR	Wabash River
U.S. Fish and Wildlife Service - Mississippi Ecological Services Field Office	Atchafalaya River

*Pallid sturgeon population assessment program (PSPAP)

Table 6.2. Sample size and time period between captures for 15 populations of shovelnose sturgeon.

		Years between captures		
Population	N	Mean	SE	Maximum
Missouri River (rkm2,523-2851)	744	3.03	0.10	17.74
Missouri River (rkm 1,328-1,416)	243	1.75	0.12	5.80
Missouri River (rkm 1,207-1,305)	80	2.13	0.09	6.25
Missouri River (rkm 789-1,207)	1454	1.89	0.03	6.03
Missouri River (rkm 402-789)	959	2.07	0.04	6.06
Missouri River (rkm 0-402)	1150	2.03	0.04	6.12
Platte River	115	1.82	0.13	12.18
Kansas River	144	2.06	0.12	5.99
Mississippi River (Pools 9 & 10)	82	0.69	0.08	3.19
Mississippi River (Pools 11 & 12)	210	1.64	0.09	7.03
Mississippi River (Pools 20-26)	80	0.73	0.05	1.97
Mississippi River (rkm 201 - OH River confluence)	457	1.58	0.06	7.12
Wisconsin River	82	1.37	0.18	4.93
Wabash River	31	4.35	0.21	7.34
Atchafalaya River	15	0.38	0.12	1.76

Table 6.3. Mean estimated length at age (± SE), and relative growth index (below estimated length at age) for shovelnose sturgeon collected throughout their distribution. Shovelnose sturgeon from the Wabash River and Atchafalaya River were not included in this analysis due to low (n = 31 and 15) sample sizes.

	Age										
	0	1	2	3	4	5	6	7	8	9	10
MO River (rkm 2523-2851)	132 (0.14) 88	166 (0.04) 88	209 (0.04) 89	247 (0.04) 89	283 (0.05) 89	315 (0.05) 90	344 (0.06) 91	371 (0.07) 91	395 (0.07) 92	417 (0.08) 92	437 (0.09) 93
MO River (rkm 1328-1416)	201 (0.88) 134	252 (2.10) 134	314 (2.18) 133	367 (2.21) 132	412 (1.00) 130	451 (1.52) 129	484 (2.37) 127	511 (2.46) 126	536 (2.69) 124	558 (0.37) 123	576 (2.5) 122
MO River (rkm 1207-1305)	171 (1.38) 114	215 (1.96) 114	267 (2.03) 114	312 (2.06) 112	350 (2.13) 111	382 (2.21) 109	410 (2.28) 108	434 (2.44) 107	454 (2.46) 105	471 (2.78) 104	485 (2.62) 103
MO River (rkm 789-1207)	191 (1.47) 128	240 (2.12) 128	298 (2.16) 126	347 (2.27) 124	388 (2.31) 123	422 (2.42) 121	451 (2.53) 119	476 (2.73) 117	496 (2.71) 115	513 (3.01) 113	527 (3.28) 112
MO River (rkm 402-789)	148 (1.21) 99	186 (1.72) 99	233 (1.76) 99	275 (1.80) 99	311 (1.84) 98	343 (1.85) 98	372 (1.97) 98	398 (2.00) 98	420 (1.97) 97	440 (2.19) 97	458 (0.27) 97
MO River (rkm 0-402)	145 (1.19) 97	167 (1.94) 89	233 (2.28) 99	268 (1.70) 96	305 (1.32) 96	339 (1.34) 97	368 (1.04) 97	393 (1.00) 97	417 (0.86) 97	435 (0.65) 96	453 (0.68) 96
MS River (pools 9 & 10)	154 (1.07) 103	193 (1.66) 103	242 (1.69) 103	287 (1.72) 103	328 (1.72) 104	365 (1.77) 104	399 (1.79) 105	430 (1.84) 106	458 (1.75) 106	484 (1.90) 107	507 (1.92) 108
MS River (pools 11 & 12)	207 (1.49) 138	260 (2.14) 138	324 (2.19) 137	378 (2.22) 136	424 (2.30) 134	465 (2.42) 133	499 (2.39) 132	529 (2.60) 130	554 (2.60) 129	575 (2.72) 127	594 (3.03) 126
MS River (pools 20-26)	259 (1.91) 173	322 (2.79) 171	393 (2.93) 167	446 (3.11) 160	487 (3.35) 154	518 (3.58) 148	542 (4.31) 143	559 138	572 133		
MS River (rkm 201 - OH River confluence)	217 (1.58) 145	272 (2.30) 145	338 (2.39) 143	391 (2.45) 141	435 (2.51) 138	472 (2.65) 135	502 (2.77) 132	527 (2.97) 130	549 (3.25) 127	566 (3.20) 125	580 (4.12) 123
Wisconsin River	113 (0.97) 76	142 (1.37) 75	178 (1.39) 75	212 (1.41) 76	243 (1.41) 77	272 (1.44) 78	299 (1.46) 79	325 (1.50) 81	349 (1.50) 81	370 (1.52) 82	391 (1.57) 83
Platte River	199 (1.52) 133	250 (2.19) 133	310 (2.26) 131	360 (2.33) 129	402 (2.49) 127	436 (2.55) 125	465 (2.66) 123	489 (2.86) 121	508 (2.71) 118	524 (3.40) 116	541 (3.97) 115
Kansas River	168 (1.31) 112	210 (1.87) 112	263 (1.91) 111	308 (1.96) 111	349 (2.03) 110	384 (2.04) 110	414 (2.15) 109	440 (2.15) 108	464 (2.34) 108	485 (2.35) 107	501 (2.34) 106

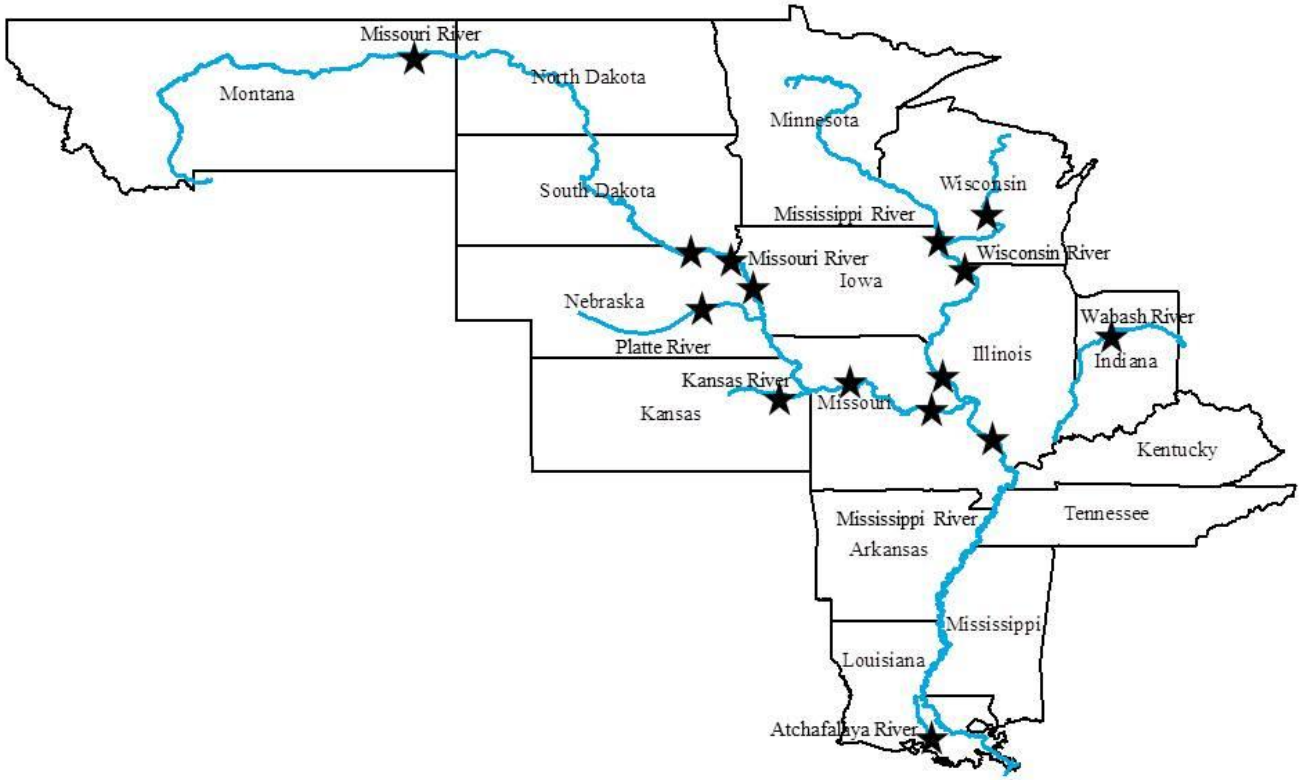

Figure 6.1. Distribution of data sources for shovelnose sturgeon used for age and growth analysis. Stars indicate the river reach from where mark-recapture data originated. See Table 1 for a list of agencies and universities that contributed data.

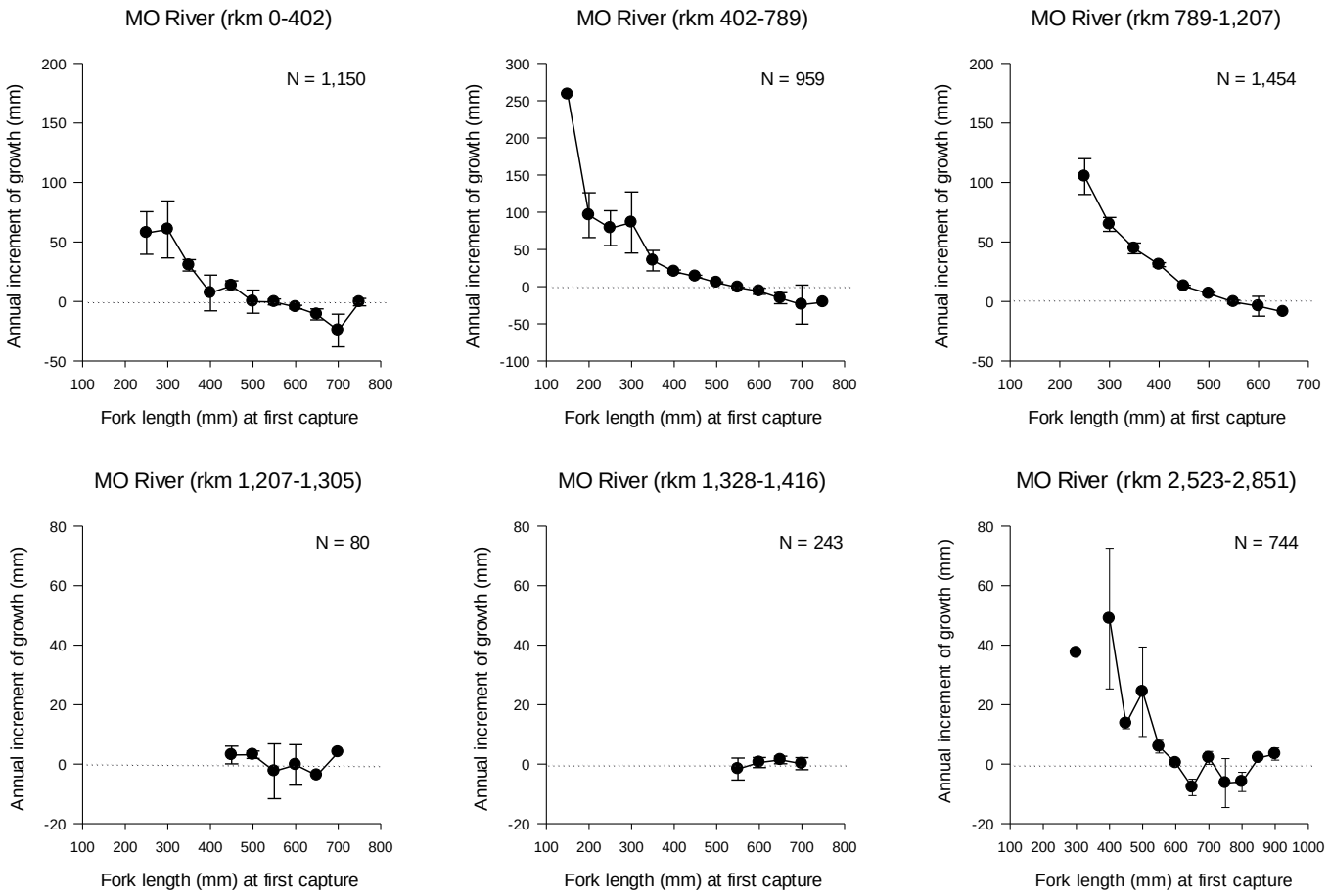

Figure 6.2. Annual increment of growth for shovelnose sturgeon throughout the Missouri River derived from mark-recapture data. Fork length at first capture relates to the initial length at tagging and the subsequent growth that has occurred thereafter.

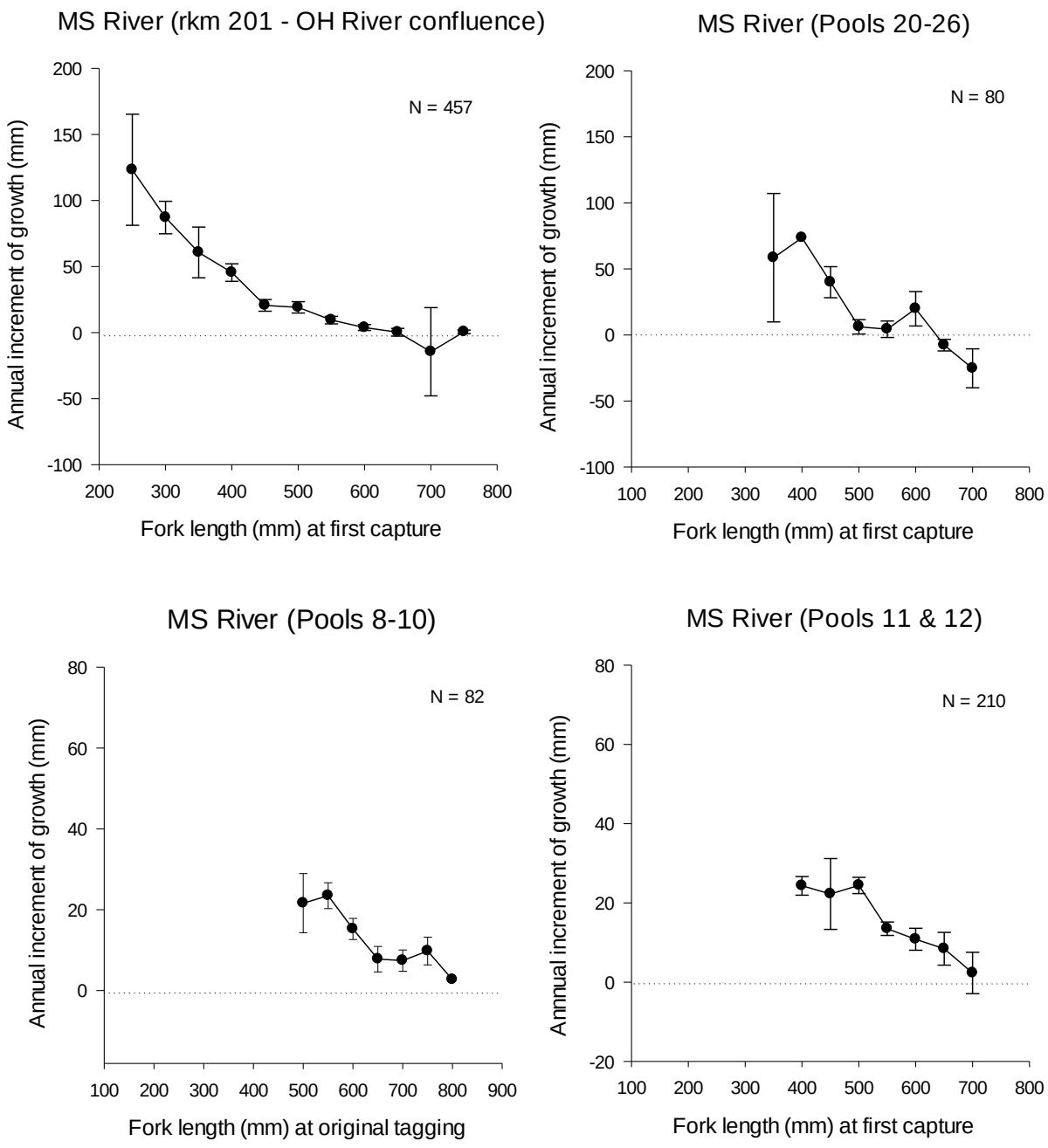

Figure 6.3. Annual increment of growth for shovelnose sturgeon throughout the Mississippi River derived from mark-recapture data.

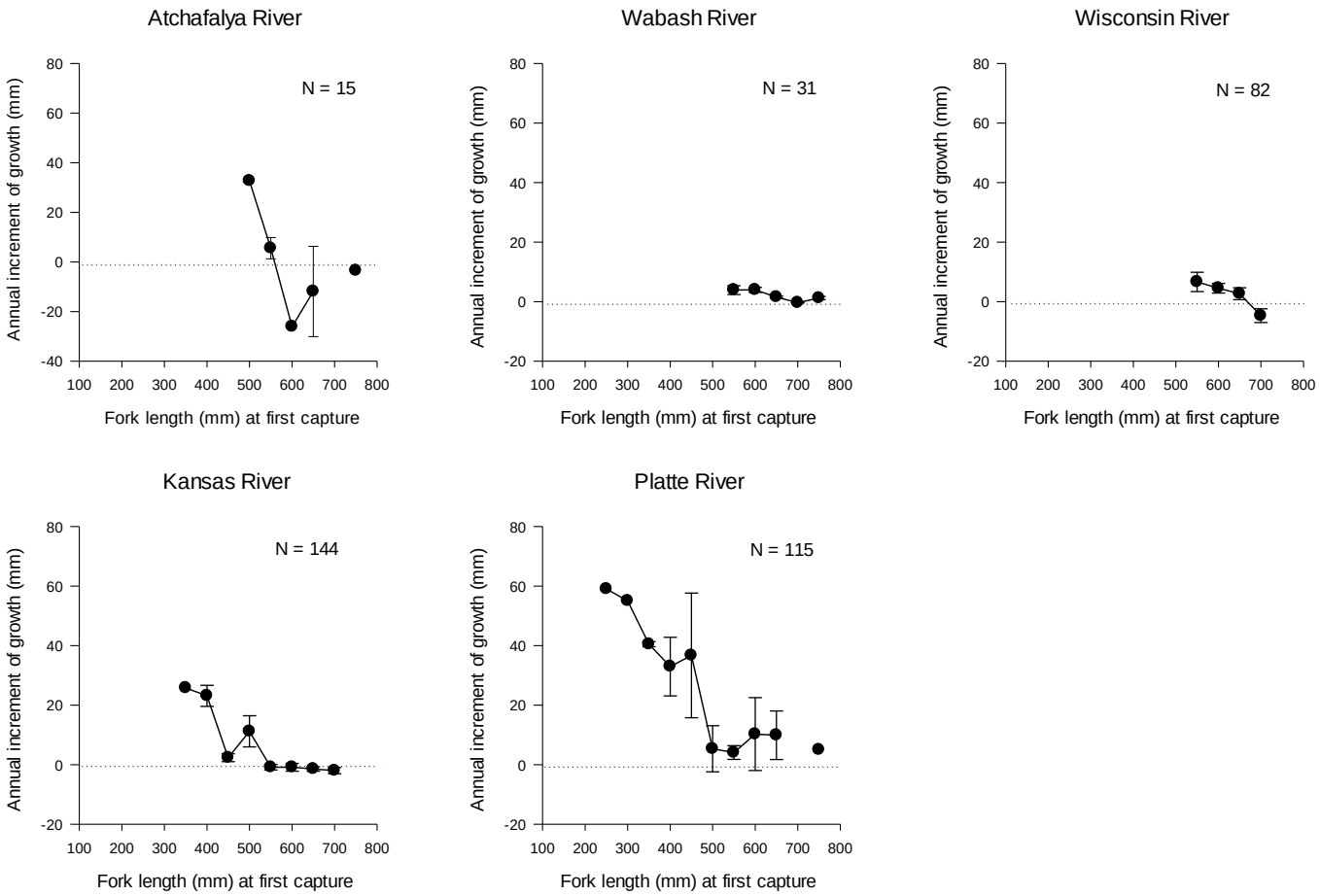

Figure 6.4. Annual increment of growth for shovelnose sturgeon throughout tributaries of the Missouri River and Mississippi River derived from mark-recapture data. Fork length at first capture relates to the initial length at tagging and the subsequent growth that has occurred thereafter.

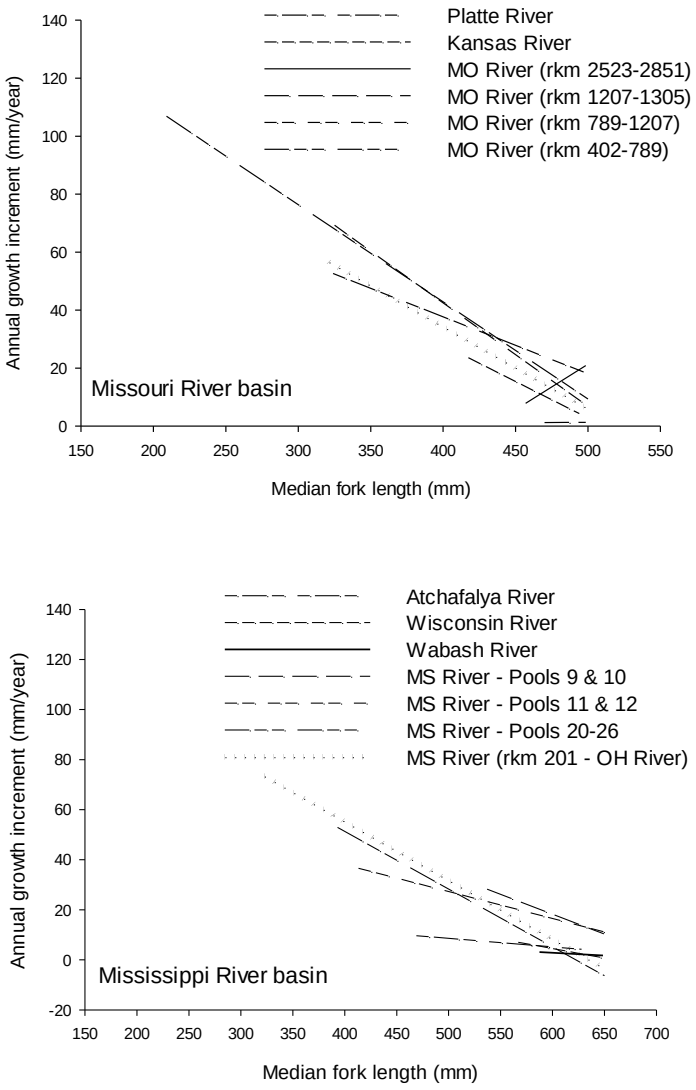

Figure 6.5. Average annual growth increment for the median fork length of shovelnose sturgeon from seven populations found throughout the Missouri River basin (top panel) and Mississippi River basin (bottom panel). Average annual growth was calculated from mark-recapture data. Growth trajectories stopped at 500 mm and 650 mm for the Missouri and Mississippi Rivers, as this is the length where most populations began to display minimal growth.

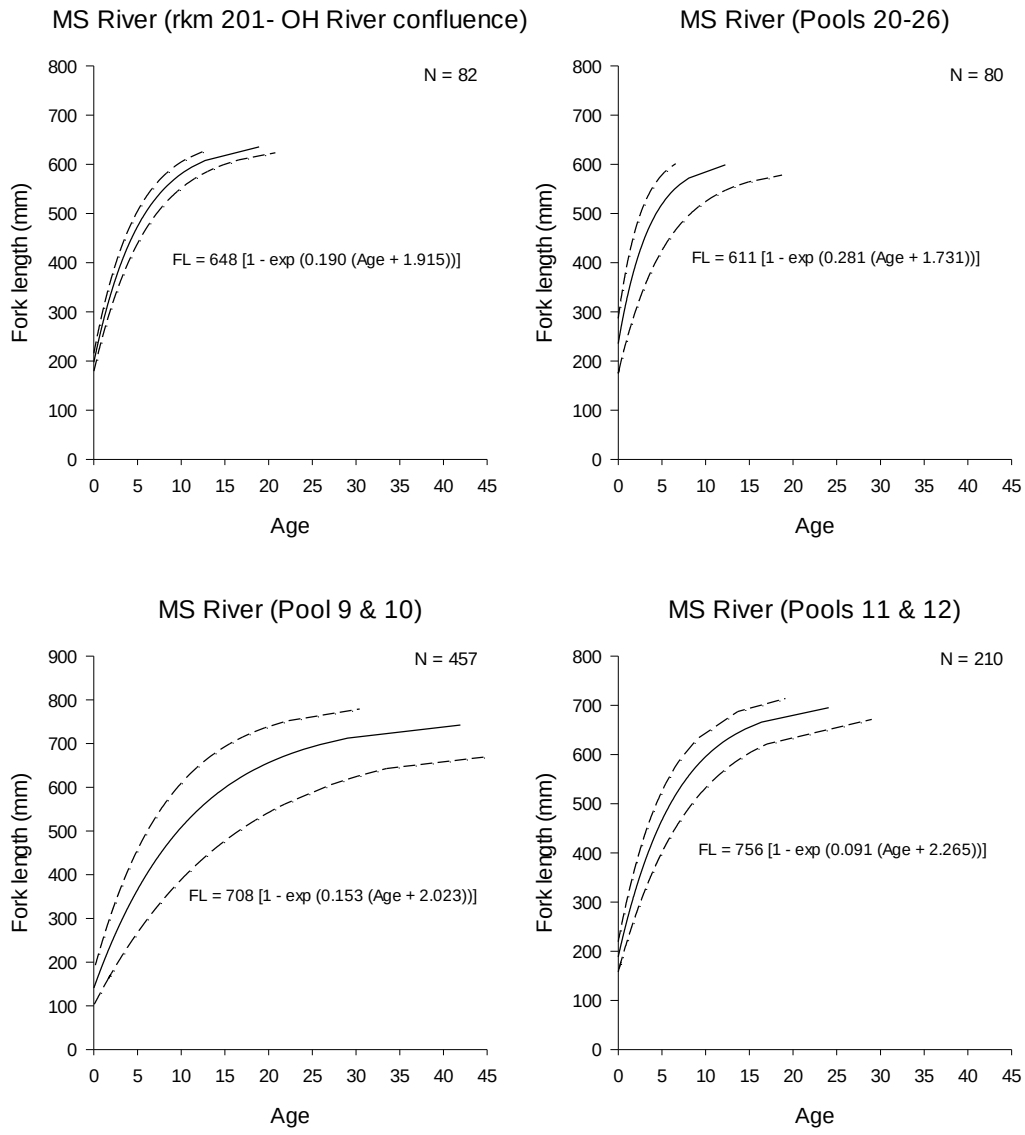

Figure 6.6. Length at age relation for shovelnose sturgeon derived from mark-recapture data from the Mississippi River. Growth increment data were fitted to a von Bertalanffy growth curve reformulated in terms of the increment of growth and the period of time between captures. Age for fish of any given size (FL) was estimated with parameters derived from tagging data. Dashed lines represent 95% confidence intervals

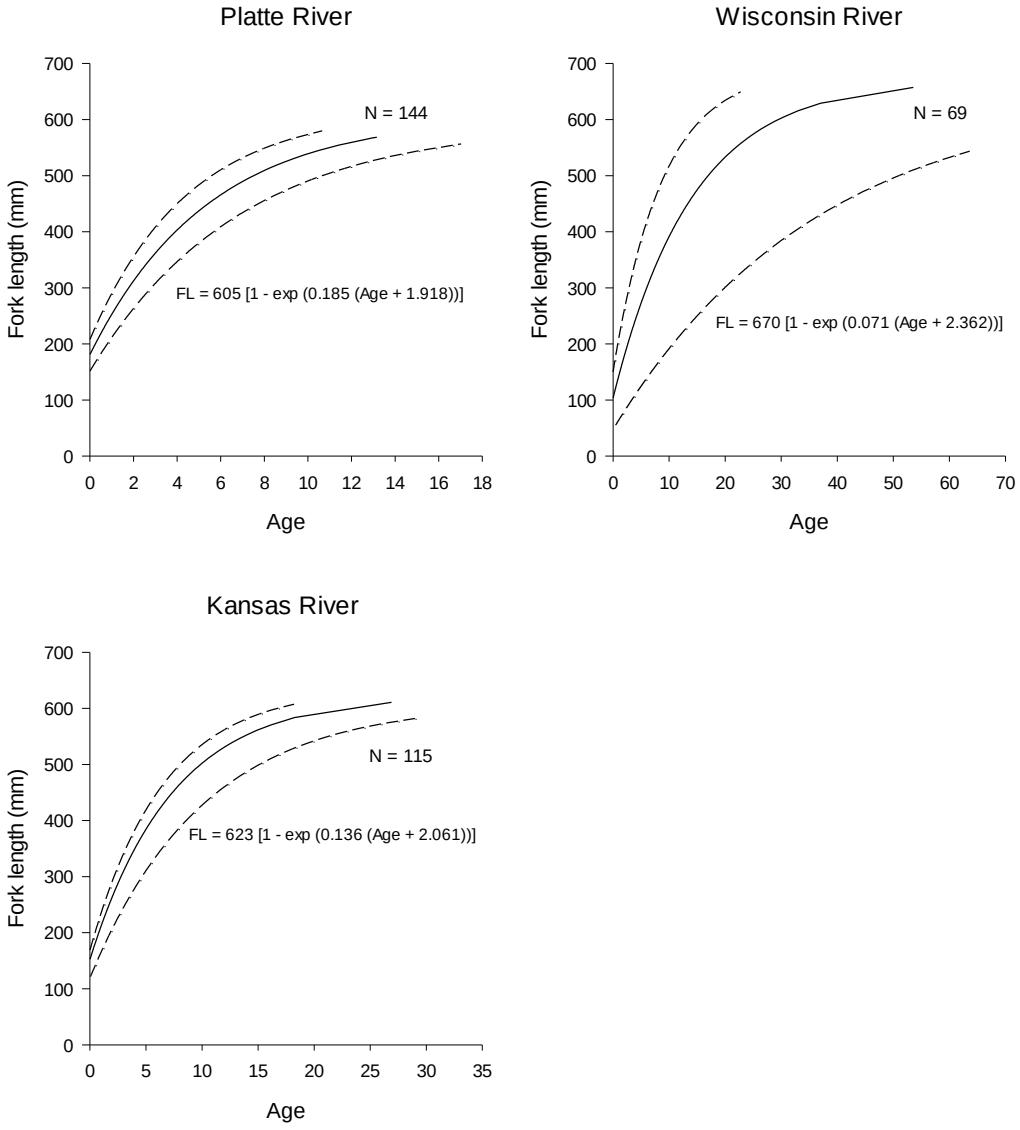

Figure 6.7. Length at age relation for shovelnose sturgeon derived from mark-recapture data from tributaries of the Missouri and Mississippi Rivers. Growth increment data were fitted to a von Bertalanffy growth curve reformulated in terms of the increment of growth and the period of time between captures. Age for fish of any given size (FL) was estimated with parameters derived from tagging data. Dashed lines represent 95% confidence intervals.

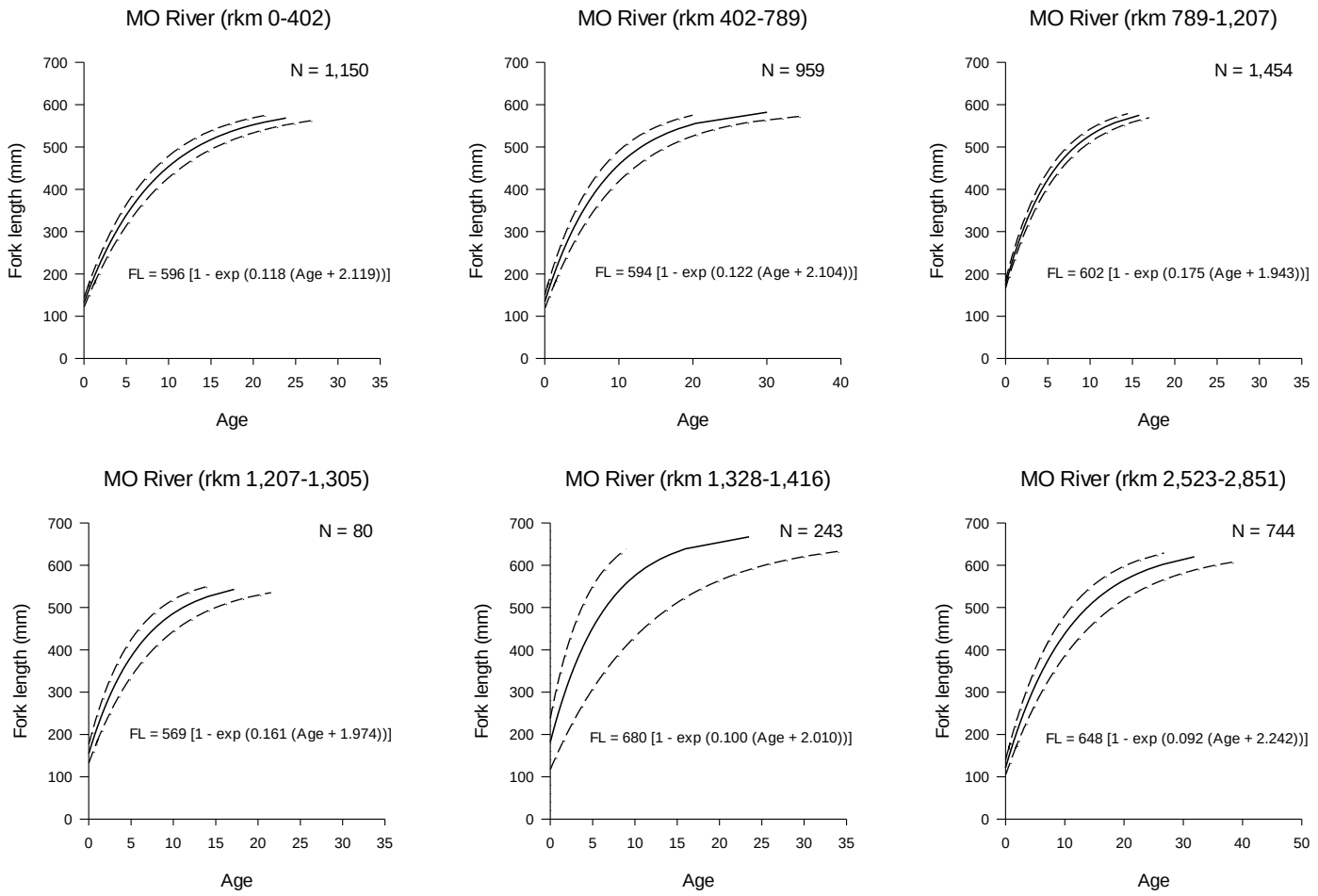

Figure 6.8. Length at age relation for shovelnose sturgeon derived from mark-recapture data from the Missouri River. Growth increment data were fitted to a von Bertalanffy growth curve reformulated in terms of the increment of growth and the period of time between captures. Age for fish of any given size (FL) was estimated with parameters derived from tagging data. Dashed lines represent 95% confidence intervals.

CHAPTER 7: CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

Human alterations to rivers and streams are commonplace and changes to the natural flow regime are considered to be one of the most serious threats to the ecological integrity of these systems. Aquatic biodiversity has been greatly reduced world-wide and future conservation will be challenging in the face of pressure to use water for urban development, industry, and agricultural practices. We have learned a great deal about the effects modified river systems have on aquatic organisms at various scales, yet challenges still exist. Focusing on rivers at a landscape scale (i.e., riverscapes; Fausch et al. 2002) has emphasized the importance of aquatic linkages across the landscape and the role that connectivity plays in maintaining species assemblages.

Sturgeons have evolved life-history traits and strategies that are well-suited for a variety of stochastic riverine environments, but have experienced marked declines due to river modification and over-harvest. Sturgeon are an ideal study subject for determining the quality of a riverine environment because specialized traits such as morphology, long life expectancy, intermittent spawning, and movement capabilities were defined by historic river conditions and population success. The condition of sturgeon populations likely translates to the amount of anthropogenic affects that have occurred in a particular river ecosystem; however, understanding sturgeon demographics and dynamics is difficult because the scale at which processes may be governed is largely unknown. Further, accurate assessments of dynamic rate functions are difficult to quantify, thereby making modeling exercises difficult when attempting to determine sustainability, harvest regulations, or population abundance.

The premise of my dissertation work was to provide important information relating to the understanding of *Scaphirhynchus* sturgeon populations that are found throughout the Missouri River and Mississippi River basins. Specifically, I was interested in determining population demographic dynamics at both local (i.e., Platte River, Nebraska) and regional scales. In light of the work presented in this dissertation, I make the following management and research recommendations (by chapter):

CHAPTER 2: POPULATION CHARACTERISTICS OF PALLID STURGEON IN THE LOWER PLATTE RIVER, NEBRASKA

- Monitoring of pallid sturgeon abundance in the Platte River should be continued. Examining long-term trends in population abundance, distribution throughout the lower Platte River, and movement between the Platte and Missouri rivers will provide important information for recovery, sustainability, and the importance of inter-connectivity between systems. Monitoring with both trammel nets and trotlines during the spring and fall is recommended. Summer sampling for pallid sturgeon is likely not needed for population monitoring, but may be important to meet other research or management objectives.
- Pallid sturgeon in the Platte River were in good condition and values (i.e., relative condition factor; *Kn*) met or exceeded values reported from the Missouri River. A food habit study for both juvenile and adult pallid sturgeon is warranted to determine if differences exist in diet between the Missouri and Platte Rivers.
- Bioenergetic modeling may provide insight into energy requirements needed for pallid sturgeon that occupy the Platte and Missouri rivers. Development of

bioenergetics requirements under varying flow conditions will shed light on the potential influence hydropeaking has on sturgeon in the Platte River.

- The Platte River is a dynamic system that has similar physical characteristics of the historic Missouri River. Telemetry work in the Missouri River has provided great insight into seasonal macrohabitat preferences in a fairly homogenous environment. Intensive telemetry efforts during the spawning season have described pallid sturgeon reproductive behaviors, movement patterns, and gross spawning locations. However, little is known how pallid sturgeon use the Platte River and the specific habitat types that are chosen both temporally and spatially. Therefore, telemetry work for both juveniles and adults is warranted. Study subjects should be caught in periods outside of the spawning season to ensure a higher probability of capturing a resident Platte River fish.
- Shovelnose sturgeon were concurrently sampled throughout this study and were found in much higher abundance. There were a total of 4,091 shovelnose sturgeon collected from 2009-2012, resulting in a catch ratio of 1:30 pallid to shovelnose sturgeon.
- Mark-recapture population estimates for pallid sturgeon were not attempted in this study due to the low percentage of recaptures. These analyses should be attempted during future monitoring work as the number of recaptures increase. An estimated 30,870 ± 2,270 shovelnose sturgeon occurred in the lower Platte River throughout this study period (Hammen, J.J., *unpublished data*). Using the catch ratio of 1:30 pallid to shovelnose sturgeon would result in approximately

926 pallid sturgeon. This estimate can be used as baseline data for future comparisons.

- Pallid sturgeon were captured at the upstream-most end of our study area and in the lower portions of the Elkhorn River. Future work in areas outside of the previously sampled Platte River (i.e., further upstream or in tributaries) may result in additional pallid sturgeon captures, particularly in years with above-normal discharge.
- Pallid sturgeon interchangeably use the Platte and Missouri rivers. A collaborative and coordinated effort between the Missouri and Platte river research projects would be beneficial for understanding important linkages that may or may not be necessary for pallid sturgeon persistence.
- The physical characteristics of the Platte River, coupled with a variable hydrological regime, create conditions that make it difficult to attain precise sampling results. Sampling gear efficiencies are unknown in the Platte River and likely vary under multiple conditions. Future research is warranted to quantify catchability for sampling gears under varying conditions.

CHAPTER 3: HYDROLOGIC VARIABILITY INFLUENCES DISTRIBUTION AND OCCURRENCE OF PALLID STURGEON IN A MISSOURI RIVER TRIBUTARY

- Pallid sturgeon occurrence in the Platte River was largely determined by both the quantity of water in the system and the diel variability in discharge (i.e., resulting from hydro-peeking). Continued monitoring of pallid sturgeon in the Platte River

throughout wet and dry years will provide additional data for model refinement and validation.

- Experimenting with flow manipulation to reduce diel flow variability or to maintain river discharge during the spring and fall would provide insight for increasing abundance and distribution of sturgeon species throughout the Platte River.
- The models used for pallid sturgeon predictions in the lower Platte River may be used for predicting pallid sturgeon occurrence further upstream. These models could aid collections efforts to focus on time periods that coincide with the greatest probability of occurrence.

CHAPTER 4: IS THAT YOUR FINAL ANSWER? USING MARK-RECAPTURE INFORMATION TO VALIDATE AND ASSESS AGE AND GROWTH OF LONG-LIVED SPECIES

- Fin rays were previously chosen to measure growth of sturgeon in the Platte River. In light of these results, I suggest that mark-recapture data be used to describe growth for both shovelnose and pallid sturgeon species in the Platte River. An establishment of growth standards would provide a means to compare and monitor growth through time.
- Continued monitoring of pallid sturgeon and shovelnose sturgeon in the Platte River will provide additional mark-recapture data needed to refine estimates of age that are predicted from the reformulated von Bertalanffy growth equation.

These age estimates can be used to describe the population age structure; information needed for modeling survival and long-term sustainability.

- Shovelnose sturgeon have recently been produced in Nebraska hatcheries. The release and subsequent recapture will provide an opportunity to perform a similar age validation study with mark-recapture data.

CHAPTER 5: SIMULATED VARIABILITY IN FIN RAY AGE ASSIGNMENTS AFFECTS POPULATION DYNAMIC RATE FUNCTIONS AND ESTIMATES OF LONG-TERM SUSTAINABILITY OF SHOVELNOSE STURGEON

- Discontinue use of fin rays for age and growth analysis of shovelnose sturgeon and pallid sturgeon. Age sensitivity analyses indicate that population dynamic rates are not accurately estimated and may result in mismanagement of sturgeon species.
- Evaluate other methods for determining population dynamic rate functions. The use of mark-recapture data to estimate rate functions where feasible is warranted.

CHAPTER 6: RANGE-WIDE AGE AND GROWTH CHARACTERISTICS OF SHOVELNOSE STURGEON FROM MARK-RECAPTURE DATA: IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

- Several populations had reduced size at maturity and lower maximum sizes. Future research to determine the causes for these patterns are warranted. Specifically, experiments directed at manipulating anthropogenic affects to

initiate plastic responses (i.e., decreased or increased size at maturity) of shovelnose sturgeon would provide important information for future management.

- Commercial harvest of shovelnose sturgeon was eliminated in areas where they are sympatric with pallid sturgeon. Shovelnose sturgeon harvest is expected to be re-directed to areas outside of the commercial harvest closure. Identification of areas with increased harvest and continued monitoring of these populations is needed. Continually tagging and recapturing fish will provide evidence if plastic physiological changes (e.g., reduced size and age at maturity) occur.
- Expansion of this analysis to areas outside of our study area would provide a complete picture of the current status and health of shovelnose sturgeon populations (i.e., lower Mississippi River and additional tributaries).
- Sturgeons are capable of making large-scale movements and the importance of connectivity between habitat types (both within and among river systems) is unknown. Fin ray microchemistry techniques have potential for reconstructing past movement patterns and determining natal origin. A previous study by Phelps et al. (2012) was successful in describing natal origin of age-0 *Scaphirhynchus* sturgeons captured in the middle Mississippi River. The origin of these fish varied from throughout the lower Missouri River (> 589 km upstream from its mouth) to the upstream portions of the Mississippi River. Expansion of this analysis throughout the entire Missouri and Mississippi River basins would provide information needed for understanding species recovery and sustainability.
- The definition of a population for this analysis was defined by the area of collection (i.e., sections of the Missouri and Mississippi Rivers or tributaries).

Previous genetic work with shovelnose sturgeon in the Platte and lower Missouri River found that these fish share a similar genetic structure and cannot be distinguished between geographic sampling locations. However, many fish in my defined populations were sampled from the same general area many years after the original capture. Size at maturity and maximum age varied and populations appeared to function independently, though in most instances there were no physical barriers. These populations appear to function as a metapopulation, where a system of discrete local populations within a larger network has partially independent dynamics, but receive some identifiable demographic influence from other populations through dispersal. Future metapopulation analyses are needed to describe how population dynamics and reproduction are affected by metapopulation structure.

- A nonequilibrium metapopulation might best describe shovelnose sturgeon at a range-wide scale (Schlosser & Angermeier 1995). This is defined where dispersal is limited in some reaches due to reduced connectivity among habitat patches. Further, deteriorating habitat quality in many other reaches may increase the rate of extinction among subpopulations. As an example, only three juvenile shovelnose sturgeon (< 510 mm) have been sampled since monitoring began in 2003 in the inter-reservoir reach of the Missouri River (rkm 1328-1415) (Shuman & Klumb 2012). This indicates that the population has very limited recruitment (i.e., sink population) and has to rely on contributions from source populations in other locations. Pools 20-26 in the Mississippi River may pose similar problems with connectedness. Lock and Dam 19 is a barrier for upstream fish passage,

potentially limiting upstream source habitats that maintain downstream subpopulations (Fausch et al. 2002). Determining source populations throughout the distribution of shovelnose sturgeon is priority because these populations may be necessary for maintaining persistence and viability.

- Population characteristics and dynamics of pallid sturgeon in the Missouri River may be similar to shovelnose sturgeon, as this species is a congener that shares similar life history characteristics. For example, a 2013 recapture of a presumed wild pallid sturgeon that was originally captured in 2001 averaged about 6-7 mm of annual growth. (K. Steffensen, unpublished data). Most adult pallid sturgeon captured in the lower Missouri River rarely exceed 1,100 mm, where historically, adult pallid sturgeon were collected in excess of 1,500 mm. Similar to shovelnose sturgeon, pallid sturgeon may be experiencing reduced maximum and asymptotic sizes resulting in a truncated age distribution. These characteristics could have potential limitations on lifetime reproductive output because truncated ages translates to fewer spawning opportunities.

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